The effect of increasing temperature on algae-fish interactions on coral reefs

Thesis submitted by
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Abstract

Increasing environmental temperature is one of the most pervasive stressors affecting ecosystems worldwide, driving shifts in species' distribution, phenology, behaviour and community composition. These changes are underpinned by the thermal sensitivities of individual species, with ectotherms, plants and algae being particularly vulnerable as the rates of their biochemical and physiological processes are governed by environmental temperature. Consequently, increasing environmental temperatures can affect the performance, distribution and abundance of individual species, leading to changes in community composition, and species interactions. To date, the majority of studies investigating the effect of increasing environmental temperature on terrestrial and marine ecosystems have focused on the performance of individual taxa or responses of assemblages, but relatively few have investigated the effect of temperature on trophic interactions. Understanding the influence of temperature on the likely outcomes of trophic interactions is key to predicting the future dynamics of ecosystems under future climate change.

Coral reefs are one of the most vulnerable ecosystems to increasing temperature as they have evolved under relatively invariable thermal environments, and many species are living in thermal environments close to their upper thermal limits. Indeed, the effect of both chronic and acute increases in temperature are already evident on coral reefs with recurrent mass coral bleaching events resulting in widespread coral mortality. These declines in coral cover have led to growing concerns that coral reefs will be increasingly overgrown by macroalgae. While herbivorous fishes are widely viewed as key to mitigating algal overgrowth on coral reefs, it is currently unknown how both the consumption and production of algal material, and hence the accumulation of algal biomass, will change under increasing temperature. The objective of this thesis was to investigate the effect of temperature on algae-

fish interactions on coral reefs. Specifically the aims of the thesis were to determine: (1) the influence of temperature on the feeding rates of herbivorous fishes while also accounting for resource availability; (2) how rates of turf algae growth and feeding rates of herbivorous fishes change with seasonal variation in temperature; (3) how predicted increases in temperature are likely to affect the growth and survival of common coral reef macroalgae; (4) how individual metabolism, feeding rates, growth and body condition of a common herbivorous fish changes with temperature.

In Chapter 2 I compared the feeding rates of three common functionally distinct herbivorous coral reef fish species (a macroalgal browser: *Naso unicornis*, a turf algal cropper: *Siganus doliatus*, and a detritivore: *Ctenochaetus striatus*) among three latitudes on the Great Barrier Reef (GBR), and between two seasons (austral spring and summer) in the northern GBR, with both comparisons spanning a temperature range of 2-3°C. To investigate the potential effects of resource availability on feeding rates I also compared feeding rates among reefs with distinct algal communities. I found strong evidence that seasonal and latitudinal variation in temperature influenced feeding rates of all three species. A 2-3°C increase in temperature across latitude and between seasons resulted in a 25-56%, 53-58% and a 10-15% increase in feeding rates for *N. unicornis*, *S. doliatus* and *C. striatus*, respectively. There was also some evidence that algal availability influenced feeding rates, however the effects were not consistent among species. The ubiquity in response to changes in environmental temperature across three species with different diets suggests temperature is an important determinant to feeding rates.

Understanding the outcome of increased temperature to algae-fish interactions is dependent on both the thermal sensitivities of algal growth, and algal consumption. In

Chapter 3 I investigated the potential for a temperature-driven trophic mismatch in the consumption and production of algal turfs. Using seasonal variation in temperature (24 - 29°C), I quantified the relative rates of turf algal growth and feeding rates of eight nominally herbivorous fishes with varying diets across three reef crest sites on Lizard Island, northern GBR. Focal species included algal croppers: *A. nigrofuscus, S. doliatus, S. corallinus, Z. scopas* and *Z. velliferum*; detritivores: *A. olivaceus* and *C. striatus*, and a macroalgal browser: *N. unicornis.* Feeding rates of the eight herbivorous fish species tended to increase with temperature, with feeding rates of all eight species being 60%-118% greater in the summer (29°C) versus the winter (24°C), and intermediate in spring and autumn (~27°C). In contrast, turf algal growth was greatest in spring and autumn and lowest in the summer. The results of this chapter suggest a temperature-driven trophic mismatch with consumption of algal turfs likely exceeding production at temperatures at or above those currently experienced during the austral summer. This trophic mismatch at higher (summer) temperatures may provide a mechanism for herbivore consumption to keep pace with predicted increases in algal cover under ongoing climate change.

While top-down processes are widely viewed as being critical in mitigating algal overgrowth on coral reefs, the likelihood of algal overgrowth under increasing temperature is also dependant on the thermal sensitivities of the algae themselves. In Chapter 4, I investigated the responses of two life stages (adult and juvenile) of a common coral reef macroalgae to predicted increases in temperature. Specifically, I exposed recently-settled propagules of the common canopy-forming macroalga *Sargassum swartzii* and adult thalli of three species of adult *Sargassum* (*S. swartzii, S. cristaefolium, S. polycystum*) to three experimental temperatures: ambient, +2°C and +3.5°C, reflective of summer minimum, mean and maximum for the northern GBR. Growth and survival of *S. swartzii* propagules were

assessed over 48 days, and the growth, physical toughness, elemental composition and susceptibility to herbivory of adult thalli were assessed after short-term exposure (2-weeks) to experimental temperatures. The growth and survival of *S. swartzii* propagules was reduced by 43% and 84% respectively, when cultured at the elevated (+3.5°C) compared to ambient temperature. Similarly, growth of all three species of adult *Sargassum* was reduced by 17-49% when cultured at the elevated (+3.5°C) compared to ambient temperature. Furthermore adult thalli of *S. swartzii* and *S. cristaefolium* cultured at elevated (+3.5°C) temperature was 50% less susceptible to herbivory. The negative effects of elevated temperatures on the growth and survival of both *Sargassum* propagules and adult thalli will likely restrict the capacity of *Sargassum* to establish in new areas, and may also threaten the persistence of existing *Sargassum* meadows under future ocean temperatures.

Temperature driven mismatches can also occur within an individual if different processes (i.e. metabolism, feeding) vary in their responses to changing temperature. In Chapter 5, I investigated how oxygen consumption, feeding rates, somatic growth and body condition of a common herbivorous coral reef fish responded to changing temperature. I exposed juvenile *Siganus doliatus* to one of four experimental temperature treatments for four weeks: 26°C, 28°C, 30°C and 32°C. The temperatures were selected to reflect the range of temperatures experienced by these fishes on an inshore reef flat of the central GBR, with an additional treatment of +2°C above the summer maximum for the region. To assess the effect of temperature to feeding rates and food choice, a cafeteria-style food choice assay was conducted, where individual fishes were offered the choice of three common macroalgae (*Sargassum* sp., *Padina* sp., *Lobophora* sp.). There were marked differences in the responses of the four metrics to temperature. While feeding rate and feeding selectivity did not differ among temperatures, oxygen consumption nearly doubled from 26°C to 32°C, somatic

growth was greatest at 28°C, decreasing significantly at both higher and lower temperatures, and body condition declined at higher temperatures. These results not only highlight the potential differences in the responses individual processes to temperature, but also that individual fishes may not be able to compensate for increased energetic demands at higher temperatures, leading to reduced growth, condition and overall fitness.

This thesis provides strong support that temperature is an important driver of both algal production and algal consumption on coral reefs. Importantly, there was a positive relationship between herbivore feeding rates and temperature when examined over temperatures that are currently experienced on the GBR. Algal growth, survival, tissue quality, and susceptibility to herbivory however, peaked at a lower temperature than feeding rates, and declined at higher temperatures they currently experience in their natural environment (i.e. summer maximums). As herbivore feeding rates generally increased with increasing temperature, suggesting that the threat of macroalgal overgrowth on coral reefs under ongoing climate change may not be as likely as previously assumed, however, it is likely to come at the cost of increased metabolic and energy demand, and potentially compromised individual fitness.

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Chapter 1: General Introduction

1.1 Climate change and ocean warming

Climate change is having a dramatic effect on marine ecosystems worldwide (Walther et al., 2002; Hoegh-Guldberg & Bruno, 2010). Increased emissions of anthropogenic CO_2 and other greenhouse gases have led to increases in sea surface temperatures (SST), changes in storm frequency and severity, decreases in oxygen concentration and ocean acidification (Doney et al., 2009; Harley et al., 2006; Schmidtko et al., 2017; Bindoff et al., 2019). Of these changing environmental conditions, increased SSTs are widely viewed as having the most pervasive and immediate effect on the marine environment (Hoey et al., 2016; Hughes et al., 2017a; Pinsky et al., 2019). Global SSTs have already increased by 1 to 1.5°C above the long term 1971 – 2000 average (NOAA, 2016), and predicted to continue to increase at an unprecedented rate (Bindoff et al., 2019). These increases in SSTs have caused shifts in geographical distribution, ontogeny, reproduction, phenology and behaviour of fishes and aquatic plants (Scheffers et al., 2016; Thackeray et al., 2016) and decreases in the abundance or loss of habitat-forming organisms, such as corals and kelp in both tropical and temperate marine ecosystems (Wernberg et al., 2016; Hughes et al., 2017b, 2018b; Filbee-Dexter & Wernberg, 2018). Importantly, changes in community composition, coupled with the thermal sensitivities of individual species, will have implications for the outcomes of trophic interactions and the functioning of marine ecosystems under ongoing climate change (Dell et al., 2011; Bruno et al., 2015; Hoey et al., 2016; Pecl et al., 2017).

Ectotherms are particularly sensitive to changes in temperature because the rates of their biochemical and cellular processes are largely governed by environmental temperature

(Brown et al., 2004). Therefore, physiological processes that are fundamental for an organism's survival (e.g., metabolism, growth, development, and reproduction) are directly affected by environmental temperature (Huey & Stevenson, 1979; Brown et al., 2004). These processes function within a species-specific thermal tolerance range beyond which the organism will die (Huey & Stevenson, 1979). Within a species' thermal tolerance range the relationship between temperature and performance is typically represented by left-skewed curve (i.e., thermal performance curve, Figure 1.1). The critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}) are the upper and lower bounds of an organism's thermal tolerance range (Figure 1.1). The performance of a trait typically increases exponentially with increasing temperature from CT_{min}, and then slows as it approaches the thermal optimum (T_{opt}): the temperature at which the highest performance of a trait is achieved. At temperatures above T_{opt}, performance declines rapidly until it reaches CT_{max} (Figure 1.1). The difference between T_{opt} and CT_{max} is the thermal safety margin, and can be used as an estimate to predict an individuals' or populations' tolerance for warming (Madeira et al., 2017; Pinsky et al., 2019). The key parameters of a thermal performance curve (T_{opt}, CT_{min}, CT_{max}) vary between processes, individuals, species and populations, but are fundamental concepts associated with temperature-mediated physiological and ecosystem change (Bruno et al., 2015; Pinsky et al., 2019). However, oxygen delivery to tissues must also increase with increased metabolic demand to avoid hypoxia or hypoxaemia (Pörtner, 2010). As oxygen availability and diffusivity is much lower in water than in air (Dejours, 1981), the performance of aquatic organisms is often constrained by their capacity to deliver adequate oxygen to tissues (*sensu* Oxygen and Capacity Limitation of Thermal Tolerance; Pörtner 2010). A mismatch between the supply and demand of oxygen to tissues can

therefore restrict the thermal performance of aquatic organisms by either reducing T_{opt} or compressing the thermal tolerance range (Pörtner & Knust, 2007; Pörtner 2010).

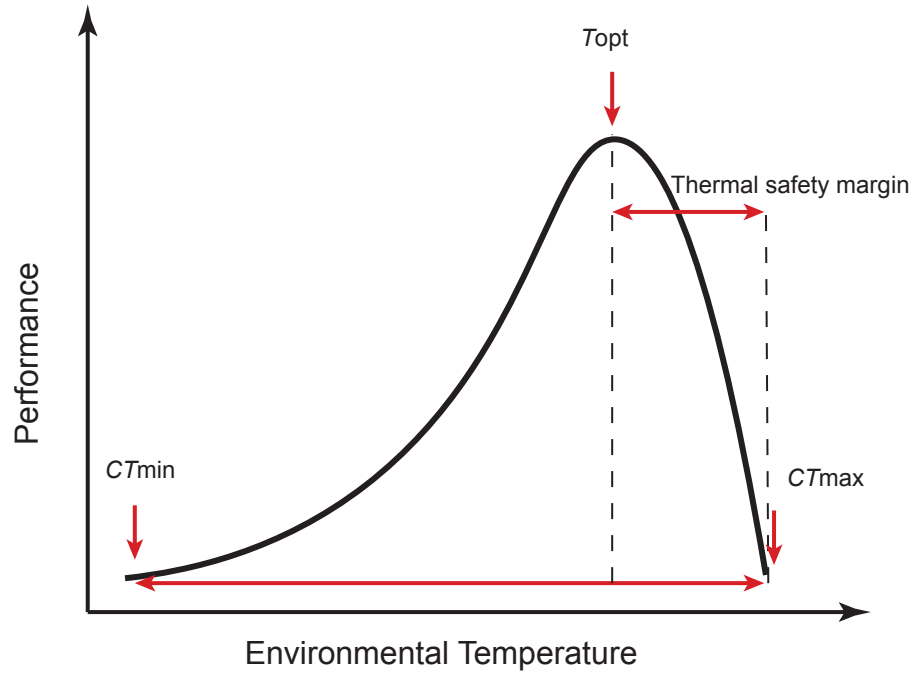

Figure 1.1 Theoretical thermal performance curve of an ectotherm, where performance increases exponentially from the critical thermal minimum (CT_{min}), until it reaches an inflection point and slows until performance reaches a thermal optimum (T_{opt}), after which it rapidly declines towards the critical thermal maximum (CT_{max}). Adapted from Huey and Stevenson, (1979) and Sinclair et al., (2016).

The physiological response of an individual to increasing temperature will depend on the shape of their thermal performance curve and the position of their local thermal environment along the thermal performance curve (Figure 1.2: Tewksbury et al., 2008; Sunday et al., 2012). For example, the thermal performance curve of tropical and polar ectotherms (thermal specialists) is often shown to be more compressed than that of temperate ectotherms (thermal generalists) as they have evolved under relatively invariable thermal environments (Tewksbury et al., 2008; Angiletta, 2009; Sunday et al., 2012). Such a

compressed thermal performance curve results in a smaller thermal tolerance range and smaller thermal safety margin (i.e., T_{opt} being closer to the CT_{max}), making tropical species more vulnerable to relatively small increases in environmental temperature than temperate species (Figure 1.2: Tewksbury et al., 2008; Sunday et al., 2012). For example, if a tropical species is currently living at or near their thermal optimum, a small increase in temperature might exceed their T_{opt} or even approach their CT_{max} causing a dramatic decline in performance (Rummer et al., 2014), or death if CT_{max} is exceeded (Habary et al., 2017; Pecl et al., 2017). Whereas for temperate species which have a both an expanded thermal performance curve and therefore a larger thermal safety margin, small increases in temperature may increase or decrease performance, but are unlikely to exceed the CT_{max} as rapidly (Figure 1.2, Sunday et al., 2012). However, it is energetically costly to maintain compensatory processes and mechanisms (i.e. genetic isoforms, epigenetics, phenotypic plasticity) which allow thermal generalists to persist within a wide thermal range (Verberk et al., 2016). Whereas, by optimizing fitness across a smaller thermal range, thermal specialists reduce energetic costs, with increased energetic potential for phenotypic plasticity and acclimation processes to long-term warming (Verberk et al., 2016).

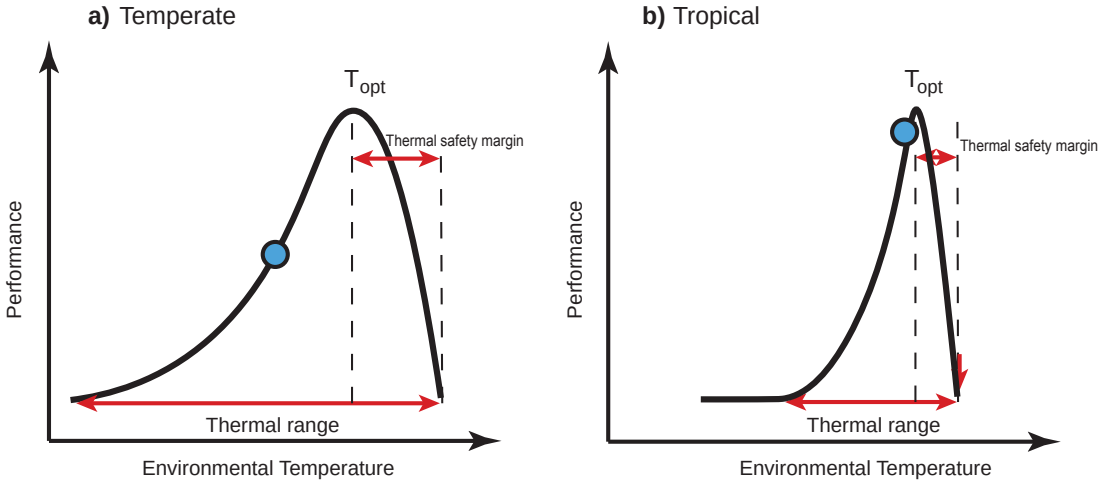

Figure 1.2: Theoretical thermal performance curves of a) temperate versus b) tropical ectotherms. The blue circle denotes the current mean temperature in relation to their thermal performance curve. Adapted from thermal performance curves of tropical and temperate lizards developed by Tewksbury et al., (2008).

The physiological effects of temperature on individual-level performance can influence species distributions, population dynamics, and trophic interactions (Brown et al., 2004; Allen et al., 2005; Dell et al., 2011; Pecl et al., 2017). Many studies have documented the response of temperature to individual processes (reviewed by Kordas et al., 2011), where growth (e.g. Brett, 1971; Cáceres-Puig et al., 2007) and metabolism (e.g. Nilsson et al., 2009; Gardiner et al., 2010; Johansen et al., 2014; Habary et al., 2017) typically increase with temperature until a thermal threshold has been reached, but the magnitude of these responses are species and taxon specific (Kordas et al., 2011). Furthermore, increasing temperatures are leading to poleward range expansions of marine taxa worldwide (Pecl et al., 2017), which have led to novel interactions between range-expanding and native species (Sorte et al., 2010). While the effect of temperature on individual-level performance and species distributions are becoming increasingly studied, few have considered how increasing temperature may impact ecological interactions (Bruno et al., 2015). This is critical because interactions between species shape the structure and functioning of ecosystems, but the

outcomes of interactions depend on the responses of individual species to increasing temperature (Brown et al., 2004; Bruno et al., 2015). Given the current and predicted increases in global SSTs (Bindoff et al., 2019), understanding how increasing temperature will influence individual performance and trophic interactions will be key to predicting the future structure and functioning of marine ecosystems.

1.2 Temperature and Plant-Herbivore Interactions

Interactions between primary producers and primary consumers (i.e., herbivores) are fundamental in structuring the algal communities of marine ecosystems (Lubchenco & Gaines, 1981; Carpenter, 1986; Hughes, 1994; Duffy & Hay, 2001). Variation in herbivory can influence the composition and/or standing biomass of local macrophyte communities, and drive changes in plant fitness and defence mechanisms (Lubchenco & Gaines, 1981; Huntly, 1991; Duffy & Hay, 2001). In relatively intact marine ecosystems, herbivores have been estimated to remove 20% of daily algal production in temperate kelp forests (Krumhansl & Scheibling, 2012), and 50-100% of daily primary production in tropical systems maintaining seagrass and algal communities in a highly productive, but cropped state (Russ, 1987; Preen, 1995; Choat & Clements, 1998; Valentine & Duffy, 2007). Ecological disturbances (i.e. marine heatwaves, storm events, eutrophication, overfishing) may cause an imbalance between algal production and consumption, which may lead to a shift to an alternate ecological state (e.g. Gardner et al., 2003; Wernberg et al., 2016)

Shifts between different ecosystem states have generally been attributed to changes in herbivory (e.g. Hughes, 1994; Hughes et al., 2007; Rasher et al., 2013; Ling et al., 2015; Vergés et al., 2016). On coral reefs for example, reductions in herbivory have been shown to limit the ability of reefs to recover following large scale coral mortality (e.g., coral bleaching,

severe storms) causing some reefs to shift from a coral- to an algal-dominated state (Lewis, 1986; Hughes, 1994; Hughes et al., 2007; Graham et al., 2015). Similarly, in temperate marine ecosystems increases in sea urchin herbivory have led to shifts from kelp-dominated to barren-dominated states (Estes & Palmisano, 1974; Estes et al., 1989; Ling et al., 2015). To date, the majority of studies investigating the influence of herbivory on algal communities have used the abundance of herbivores as a proxy for feeding intensity (Lubchenco & Gaines, 1981; Lewis & Wainwright, 1985; Vermeij et al., 2010; Adam et al., 2011), and have not considered the potential influence of other environmental factors (such as temperature) on the interaction between the production and consumption of plant communities. Given the importance of herbivory in influencing benthic communities across tropical and temperate marine ecosystems and the current and predicted increases in SSTs, understanding how marine plant-herbivore interactions are influenced by increasing temperature will be critical. In particular, how the production and consumption of algae will scale with increasing temperature, and hence influence the composition of future algal communities of marine ecosystems (Bruno et al., 2015).

1.3 Temperature and Trophic Mismatch

Should production and consumption of algae scale at the same rate with changing temperature, there should be no effect to the algal biomass in the ecosystem (Figure 1.3a). However, the balance between herbivore consumption and algal production is likely to become mismatched as temperatures increase as the thermal responses of algae (limited by carbon fixation in photosynthesis) and herbivores (limited by cellular respiration) are likely to differ as cellular respiration is generally more sensitive to changes in temperature (Allen et al., 2005; López-Urrutia et al., 2006; O'Connor, 2009; Bruno et al., 2015). Broadly, there are three different scenarios by which mismatches in response to temperature between trophic

levels may occur: differences in the (i) magnitude of responses, (ii) the rate of the responses, or (iii) thermal optima, or a combination of these scenarios (Figure 1.3b-d; Dell et al., 2014). A difference in the magnitude of response may indicate that one species performs better overall than another species across their thermal ranges. For example, if the rate of algal production is higher than the rate algal consumption and the difference between these rates does not vary with temperature, algae will dominate the ecosystem, such as in kelp forests (Figure 1.4b). Alternatively, consumers and producers may have a similar thermal range and optimum, but differ in the rates at which they approach their optimum (Figure 1.3c; Kordas et al., 2011). If, for example, algal production and its consumption have the same performance at a shared thermal optimum, but differ in the rate at which they arrive at that optimum then each temperature away from the shared optimum will likely yield a different standing biomass of algae (Figure 1.3c). Lastly, mismatches in response to temperature may also be caused by differences in the thermal optima of consumers and producers (Figure 1.3d; Pörtner & Farrell, 2008). If algal production has a higher thermal optimum than algal consumption, then at low temperatures consumption should exceed production, while at higher temperatures production should exceed consumption (Figure 1.3d, Mertens et al., 2015). Such mismatches are not limited to trophic interactions (i.e., between organisms), but may also occur within an organism (i.e., metabolic mismatch), as separate metabolic processes within an individual also have different energy requirements (Dell et al., 2014). Understanding the influence of temperature on potential metabolic and trophic mismatches is an important and complex aspect to consider when attempting to predict community responses to ocean change (Dell et al., 2014; Bruno et al., 2015).

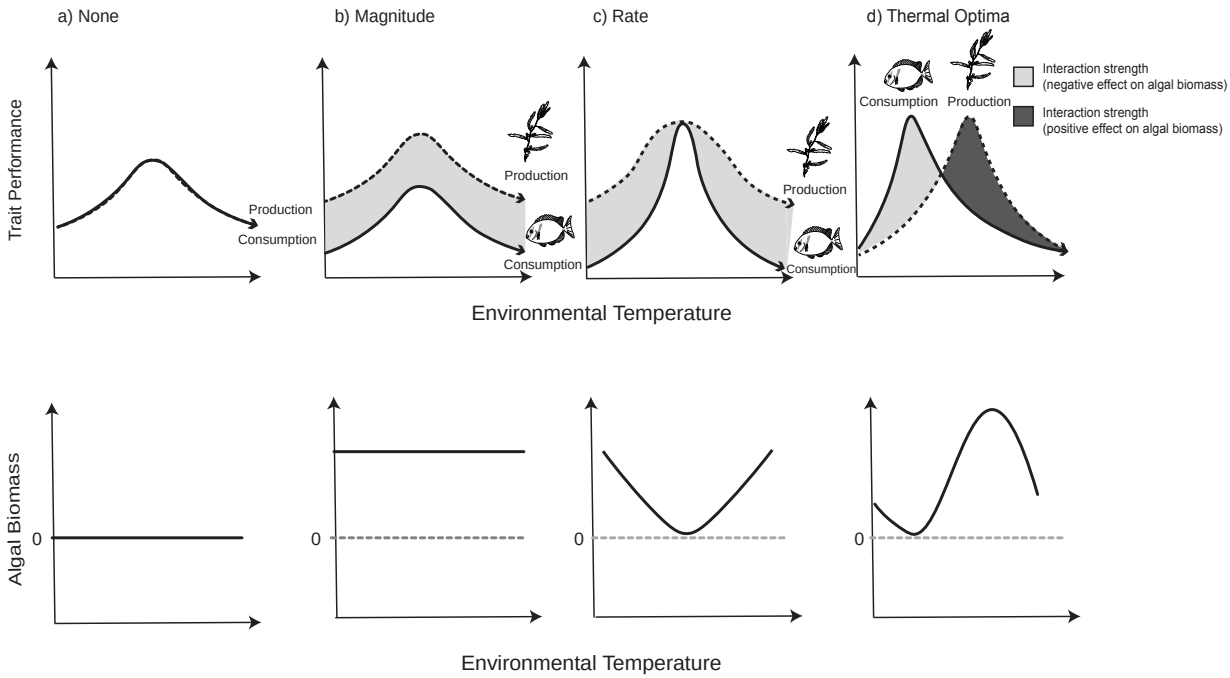

Figure 1.3: Three different scenarios by which asymmetries in response to temperature between plant consumption (solid line) and plant production (dotted line). The area between the two curves denotes trophic interaction strength with the light grey shade indicating top down control by the consumer, and the dark grey shading indicating bottom up control by the resource. Adapted from Dell et al., (2014).

In general, feeding rates of herbivores increase at a greater rate than algal growth under moderate increases in temperature. For example, feeding rates of tropical herbivorous fishes can increase by 25-100% between winter and summer (~5°C difference in temperature: (Carpenter, 1986; Polunin & Klumpp, 1992; Ferreira et al., 1998), in upwelling areas (+8°C: Smith, 2008) and in lower latitudes (+9°C: Floeter et al., 2005). Experimental increases in temperature (winter to summer temperatures: +10°C) have also resulted in 48-54% increase in feeding rates of temperate and subtropical marine invertebrates (Carr & Bruno, 2013; Gutow et al., 2016). Conversely, understory turf- and fleshy tropical macroalgae have been shown to increase growth by only 10-25%, and subtropical algae exhibit little change in growth under moderate warming (+2-4°C: e.g. Gouvêa et al., 2017; Graba-Landry et al., 2018; Hernández et al., 2018). Therefore, it would be predicted that herbivore consumption

may be more constrained by temperature than algal growth, leading to increased consumption relative to algal growth under warming. Rates of consumption by temperate marine invertebrates has been shown to exceed rates of production of phytoplankton and macroalgae (up to 2.5-fold) under small increases in temperature (+2-3°C) from the summer mean (O'Connor et al., 2009; Mertens et al., 2015; Gutow et al., 2016) leading to potential dietary resource limitation for consumers into the future. However, under greater increases from the summer mean (+4°C), Mertens et al., (2015) found that algal production in intertidal rocky reefs could persist where herbivore consumption could not, offering a potential herbivory-free refuge at elevated temperatures. Therefore, understanding the relative thermal sensitivities between consumption and production of algae can give insight on future ecosystem structure under warming (Bruno et al., 2015). However, to-date there are no studies investigating how temperature may influence the relationship between algal growth and herbivore consumption in tropical marine systems.

1.4 The effects of temperature on coral reef herbivory

Coral reefs are one of the most biodiverse, but threatened ecosystems (Walther et al., 2002). Along with other low latitude biomes, coral reefs are predicted to be particularly sensitive to increasing temperature as they have evolved under relatively invariable thermal conditions and as such, tropical ectotherms typically have compressed thermal performance curves and reduced thermal safety margins (Tewksbury et al., 2008; Sunday et al., 2012). Although coral reefs are warming at about 70% the rate of average global SSTs (Lough, 2012), small to moderate increases in temperature (1 to 1.5°C above the mean summer SST) can cause serious and lasting habitat loss and degradation through mass coral bleaching (Jokiel & Coles, 1990; Hughes et al., 2003, 2017a; Hoegh-Guldberg & Bruno, 2010). Indeed, the unprecedented back-to-back bleaching events of 2016 and 2017 on Australia's Great Barrier

Reef have led to extensive and widespread coral mortality and subsequent recruitment failure (Hughes et al., 2018b, 2019). Benthic organisms, predominately turf- and macroalgae rapidly recruit to the dead coral skeletons (Diaz-Pulido & McCook, 2002; Leggat et al., 2019), which have led to concerns of increased algal biomass on coral reefs (Bellwood et al., 2004). The threat of algal overgrowth on coral reefs is also dependent on the relative rates of consumption versus algal growth in response to temperature, which have yet to be considered when predicting the future functioning of coral reefs.

To-date, very few studies have investigated the relative influence of temperature to the algal production and its consumption (hence, algae-fish interactions) on coral reefs. A growing number of studies from temperate marine ecosystems have shown that as an overall trend, herbivore consumer pressure increases with warming within the sub-lethal temperature range, but decreases past a thermal threshold (O'Connor, 2009; O'Connor et al., 2009; Poore et al., 2013; Mertens et al., 2015; Gutow et al., 2016). The limited number of studies that have investigated the effect of temperature to herbivore feeding found consumption rates can increase by 25-100% under seasonal and temporal increases in temperature (Carpenter, 1986; Polunin & Klumpp, 1992; Ferreira et al., 1998; Smith, 2008), whereas turf algal biomass accumulation is lowest in the summer and winter (GBR reef crest: Klumpp & McKinnon, 1989). However, these studies were limited to one or two species, and only two to three temperatures have been compared, and the potential influence of dietary resource abundance is absent. Yet, the differential responses to temperature between consumer and resource suggest a potential trophic mismatch in favour of herbivore consumption under warming, but this relationship has yet to be investigated.

1.5 Aims and thesis outline

Understanding how algae-fish interactions may be influenced by increasing temperature is critical to predict the future structure and functioning of coral reef ecosystems. Both algal growth and its consumption are expected to increase with small increases in temperature, but how these processes vary between species, and trophic levels, and therefore the likely outcomes of future algae fish interactions, are unknown. The overall objective of this thesis, therefore, was to investigate the influence of temperature on algae-fish interactions on coral reefs. Specifically the aims of the thesis were to determine: (1) the relative influence of natural variations in water temperature on the feeding rates of herbivorous fishes; (2) how rates of turf algae growth and feeding rates of herbivorous fishes change with seasonal variation in temperature; (3) how predicted increases in temperature are likely to affect the growth and survival of common coral reef macroalgae; (4) how individual metabolism, feeding rates, growth and body condition of a common herbivorous fish changes with temperature.

These aims were addressed in the following five chapters. **Chapter 2** investigated the influence of natural variation in temperature versus resource availability in influencing herbivore feeding rates by quantifying feeding of three functionally distinct herbivores among three latitudes and two seasons on the Great Barrier Reef (GBR), and among reefs with distinct algal communities. **Chapter 3** expanded on the findings of Chapter 2, and investigated how seasonal variation in temperature influences the relative rates of herbivore feeding and turf algal growth in the northern GBR. **Chapter 4** used experimental manipulation of temperature to investigate the influence of increasing temperature on the growth, survival, tissue quality and susceptibility to herbivory of adult and juvenile life stages of the common coral reef macroalgae *Sargassum*. **Chapter 5** used juvenile *Siganus doliatus*,

a common herbivorous reef fish, to investigate the effect of rearing temperature on both physiological (i.e., oxygen uptake, feeding rate, growth and body condition), and behavioural processes (i.e. feeding selectivity).

Chapter 2: Seawater temperature influences the feeding rates of herbivorous fishes on coral reefs[1]

2.1 Introduction

Interactions between primary producers and their consumers (i.e., herbivores) are fundamental in structuring aquatic and terrestrial ecosystems (Lubchenco & Gaines, 1981; Huntly, 1991; Duffy & Hay, 2001). Through their feeding activities, herbivores moderate the abundance, standing biomass and composition of plant assemblages, and the flux of nutrients and other materials throughout an ecosystem (Dell et al., 2011). In terrestrial savannahs and grasslands and tropical marine ecosystems with relatively intact herbivore assemblages, it has been estimated that 50-100% of daily primary production is removed by herbivores, maintaining plant and algal communities in a highly productive, but cropped state; a grazing lawn (Russ, 1987; McNaughton, 1985; Choat & Clements, 1998; Gruner & Mooney, 2013). However, marked reductions in the abundance or feeding activity of herbivores can result in shifts to different ecological states dominated by larger, less productive and less palatable plants, such as woody species in terrestrial systems, or large canopy-forming macroalgae in tropical marine systems (e.g. Dublin et al. 1990; Dobson and Crawley 1994; Hughes et al. 2007). To date, the vast majority of studies investigating the importance of herbivory in shaping primary producer communities have focused on changes in the population size of herbivores (Lubchenco & Gaines, 1981; McNaughton et al., 1989; Cyr & Face, 1993; Olff & Ritchie, 1998), fewer studies have considered the potential influence of environmental conditions, namely temperature, on rates of herbivory (O'Connor et al., 2011; Bruno et al., 2015; but see: Carpenter 1986, Polunin & Klumpp 1992, Ferreira et al. 1998, Floeter et al.

[1] Graba-Landry, A., Loffler, Z., McClure, E., Pratchett, M. S., Hoey, A. S. Seawater temperature influences the feeding rates of herbivorous fishes on coral reefs (*In Prep*).

2005). Given that global temperatures are increasing at an unprecedented rate (Bindoff et al., 2019), understanding the influence of temperature on rates of herbivory is critical.

In marine ecosystems the majority of herbivores are ectotherms, and as such the rates of their cellular and physiological processes (e.g., metabolism and growth) are dependent on environmental temperature (Huey & Stevenson, 1979). The relationship between the rate of such processes (or performance) and temperature is non-linear, and is typically represented by a left skewed curve such that performance peaks at a thermal optimum, declines rapidly at temperatures above the thermal optimum and declines more gradually at temperatures below the optimum (Huey & Stevenson, 1979). Therefore, the effect of changing temperature on the performance of ectothermic herbivores will depend on how close current environmental temperatures are to their thermal optimum, and whether temperature increases will exceed their thermal optimum (Brown et al. 2004; Tewksbury et al., 2008; Sunday et al., 2012; Bruno et al., 2015).

At elevated temperatures herbivores may compensate for increased metabolic demand by increasing food intake or consuming higher quality/more nutritious food sources (Mattson, 1980; Huntly, 1991). Indeed, experimental studies have documented increased feeding rates of temperate marine invertebrate and piscine herbivores in response to small increases (+2-4°C) in temperature (Horn & Gibson, 1990; O'Connor, 2009; Carr & Bruno, 2013; Mertens et al., 2015; Gutow et al., 2016; Straub et al., 2016). However, larger increases in temperature (+7-12°C) have been shown to lead to decreases in feeding rates of temperate marine invertebrate herbivores (Lotze & Worm, 2002; Mertens et al., 2015) suggesting that the experimental temperatures may have exceeded their thermal optimum or that individuals may have reduced activity to conserve energy. Similarly, feeding rates of some herbivorous fishes

in tropical rocky reef and marginal coral reef environments have been shown to vary among seasons (Ferreira et al., 1998) and between upwelling and non-upwelling environments (Smith, 2008) presumably due to changes in water temperature. There have, however, been very few studies investigating the influence of temperature on feeding rates of herbivorous fishes on coral reefs (Carpenter, 1986; Polunin & Klumpp, 1992; Ferreira et al., 1998; Floeter et al., 2005), and all of these studies have been limited taxonomically, generally only considered two to three temperatures, and failed to account for differences in the availability of dietary resources. Increases in the availability of dietary resources can influence herbivore foraging success by reducing the search time to locate a resource (Dell et al., 2014). Therefore, predicting the influence of environmental temperature on rates of herbivory by coral reef fishes requires an understanding of thermal sensitivities over a range of different types of feeders, using multiple comparisons of temperatures, while also accounting for dietary resource availability.

Increasing ocean temperatures associated with anthropogenic global heating have resulted in regional reductions in live coral cover with growing concerns that coral reefs will be overgrown by other benthic taxa, including turf- and macroalgae that rapidly colonise dead coral skeletons (Diaz-Pulido & McCook, 2002; Hughes et al., 2018b; Leggat et al., 2019). The capacity of a coral reef to resist macroalgal overgrowth is largely dependent on the feeding behaviour of herbivorous fishes (Hughes et al., 2007; Rasher et al., 2013). The objective of this study was to test the effect of temperature to the feeding rates of nominally herbivorous fishes on coral reefs while also accounting for variation in algal (dietary resource) availability. Specifically, I compared the feeding rates of three common herbivorous coral reef fishes with distinct diets among temporal (seasonal) and spatial (latitudinal) temperature gradients, and reefs with distinct algal communities. I hypothesized

that feeding rates would increase with temperature, provided that algal availability was not limiting (Huey & Kingsolver, 2019).

2.2 Methods

2.2.1 Study Species

This study was conducted on Australia's Great Barrier Reef (GBR), comparing feeding rates of nominally herbivorous fishes (Perciformes: Acanthuridae and Siganidae) spatially and temporally. The three study species selected were common on reefs across and along the GBR, and represented distinct feeding groups: i) *Naso unicornis* (Forsskål 1775), a macroalgal browser, which consumes predominately foliose and leathery brown macroalgae (Choat et al., 2002); ii) *Siganus doliatus* (Guérin-Méneville 1829-38), a turf algae cropper, which consumes a diversity of filamentous, corticated, and foliose macroalgae (Hoey et al., 2013); and iii) *Ctenochaetus striatus* (Quoy and Gaimard 1825), a detritivore which targets detritus, diatoms and calcareous sediments (Choat et al., 2002). The primary feeding substrata for *S. doliatus* and *C. striatus* is the epilithic algal matrix (EAM), however, each species targets different components within the EAM (Choat et al., 2002; Hoey et al., 2013).

2.2.2 Study Sites

To investigate the effect of water temperature on herbivory I compared feeding rates of herbivorous fishes among three latitudes and two seasons (summer and spring) on the GBR. Feeding rates of three study species were quantified at three reef crest sites across two mid-shelf reefs within the northern (low latitude), central (mid latitude) and southern (high latitude) GBR (Figure 2.1a) during the austral summer. These locations spanned 1,200 km along the GBR with summer water temperatures (mean (± SE)) at the time of the feeding observations being 29.33°C (± 0.03), 28.15°C (± 0.02), and 26.6°C (± 0.04) in the

northern, central, and southern GBR locations, respectively. Feeding rates of these three species of herbivorous fishes were also compared between the austral spring (October: 27.08°C (± 0.05)), and austral summer (January: 29.33°C (± 0.03)) at three sites across two mid-shelf reefs in the northern GBR, representing a similar (~2-3°C) temperature range as the latitudinal study.

To determine the potential effect of resource availability on feeding rates, I also compared feeding rates of the three fish species at two reefs within each of three shelf positions (inner-, mid- and outer-shelf) during the austral spring in the northern GBR (Figure 2.1b). *S. doliatus* is rare on outer-shelf reefs in this region (Hoey et al., 2013), and therefore feeding observations for this species were only conducted in inner- and mid-shelf reefs. These shelf positions were chosen as there are large differences in the availability of algal resources across the continental shelf. Cover of leathery brown macroalgae, predominately *Sargassum* spp. (Ochrophyta: Phaeophaceae), the predominant dietary target of *N. unicornis* (Choat et al., 2002) can exceed 50% on inner-shelf reefs, yet is rare or absent (< 0.5% cover) on mid- and outer-shelf reefs (Wismer et al., 2009; Hoey & Bellwood, 2010). Conversely, the cover of the epilithic algal matrix (EAM) the primary feeding substrata for many herbivorous fishes, including *S. doliatus* and *C. striatus* (Choat et al., 2002, Wilson et al. 2002) is lowest on inner-and outer-shelf reefs (10-20% cover) and greatest on the mid-shelf reefs (~30% cover: Wismer et al. 2009).

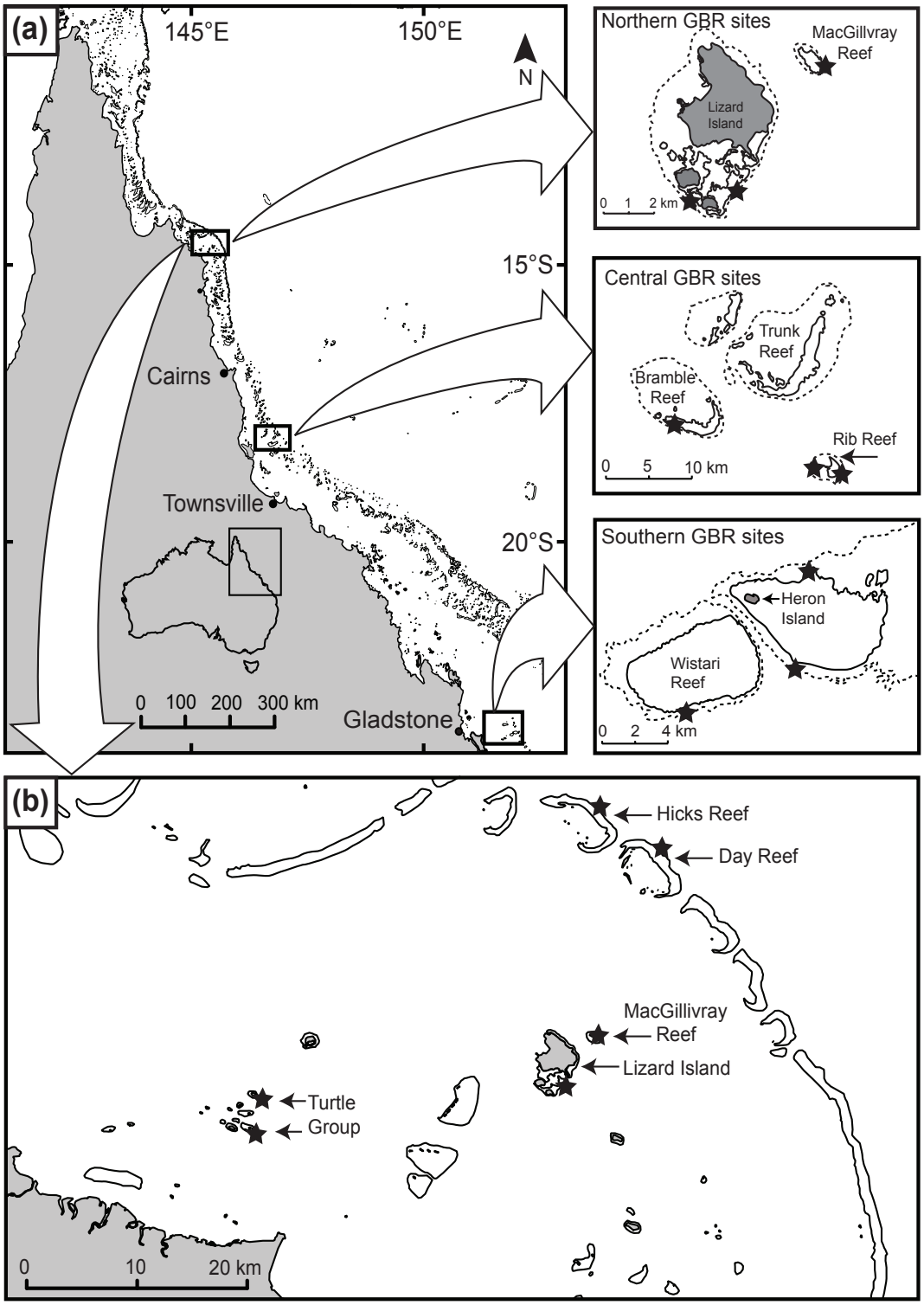

Figure 2.1: Map of the Great Barrier Reef (GBR) showing the approximate location of the reef crest sites used to quantify feeding rates of herbivorous fishes. (a) three sites within each of the three latitudes along the GBR and (b) six reefs across the continental shelf in the northern GBR. Outer-shelf reefs: Day Reef and Hicks Reef; mid-shelf reefs: Lizard Island and MacGillivray Reef; inner-shelf: Turtle Group (north and south). Black stars indicate the approximate location of the individual study sites.

2.2.3 Feeding Rates

At each site at each latitude, season and shelf position, feeding rates were quantified for a minimum of 30 individuals for each of the three study species. All feeding observations were conducted by snorkelling. An individual fish of a target species was haphazardly selected and its body length (total length, TL) estimated to the nearest centimetre. Prior to commencing observations, all observers visually estimated the length of pieces of PVC of known length (range: 10-50 cm) placed along the reef crest until estimates were within one centimetre of the known length. After a 30 second acclimation period, each individual was followed for 3 minutes during which the number of bites and the feeding substratum was recorded. Three minutes was chosen as it would encompass multiple foray events (Kelly et al., 2017) and has been used extensively to quantify feeding rates of coral reef fishes (Berumen et al., 2005; Keith et al., 2018; Pratchett, 2005; Robinson et al., 2020), including herbivorous species (Kelly et al., 2017; Hoey, 2018; Robinson et al., 2020). If a focal fish displayed any altered behaviour due to diver presence, the observation for that individual was terminated. Care was taken not to re-survey the same individual by noting specific markings and size of individual fishes, and observers always moved in one direction along the reef between successive observations (Keith et al., 2018). All feeding observations were conducted on snorkel between 10:00 hrs and 15:30 hrs to account for potential diurnal variation in feeding behaviour (Zemke-White et al., 2002).

2.2.4 Resource availability, benthic composition and herbivore assemblages

To determine the relative effect of resource availability to the feeding rates of the three study species, and any potential influence of co-occurrence among herbivorous fishes, benthic and herbivorous fish assemblages were quantified along four replicate 50 m transects at each site. Adjacent transects were separated by a minimum of 10 m. These

surveys were conducted at the same time as the feeding observations. An observer (always AGL across latitude, ECM across the continental shelf) recorded the species and total length of all roving nominally 'herbivorous' fishes > 10 cm TL within a 5m wide belt while simultaneously deploying the transect tape (following Hoey et al., 2011). Care was taken not to resurvey fish that left and subsequently re-entered the transect area. A second observer recorded the substratum immediately under the transect tape at 0.5 m intervals. The substratum was categorised as sand, rubble, EAM, live hard coral, soft coral, macroalgae, crustose coralline algae or sessile benthic invertebrates. Detailed methods and results for benthic and herbivore community analyses are provided in Appendix A (Figures A6, A7, Tables A8, A9).

2.2.5 Statistical Analysis

Bayesian generalized linear mixed models were used to analyse differences in feeding rates and resource availability among latitudes, seasons, and shelf positions. All analyses were conducted using R (version 3.5.2: R Development Core Team, 2016), and Markov chain Monte Carlo sampling (Carpenter et al., 2017) were used to fit models in STAN (Stan Development Team, 2018) using the rstanarm package (version 2.17.4: Goodrich et al., 2018). Model selection was conducted by comparing Leave One Out Information Criterion values (Vehtari et al., 2017). Collinearity between factors was determined using the 'vif' function using the car package (version 3.0.4, Fox & Weisberg, 2019). The tidybayes (version 1.0.4: Kay, 2019), broom (version 0.5.1: Robinson & Hayes, 2018) and coda (version: 0.19.2: Plummer et al., 2006) packages were used to summarise model outputs using highest posterior density (HPD) credible intervals with a probability of 95%. Plots were produced using ggplot2 within the tidyverse package (version 1.2.1: Wickham, 2016).

To analyse differences in feeding rate among latitudes, individual generalized linear mixed effects models 'stan_glmer' were used for each fish species. The models included latitude and centred total length (TL) as fixed factors, and observer as a random intercept in the model to account for any variation between observers. Cover of EAM and/or macroalgae was not included in these models as they were collinear with latitude. Therefore, separate individual models for feeding rate of each species versus latitude, and feeding rate versus cover of EAM were compared and latitude was a better predictor for variation in feeding rates of all three species (Table A1). A similar model was used to analyse differences in feeding rates across the continental shelf (Shelf Position and centred TL as fixed factors and Observer as a random factor) and between seasons (Season, TL, and EAM cover as fixed factors and Observer as random intercept). Cover of EAM and/or macroalgae was not included in the cross-shelf models as they were collinear with shelf position, and cover of macroalgae was not included in the seasonal models as it was low (<1% across all transects) and consistent between seasons (Figure 2.3). Continuous predictors for the seasonal model (i.e. Total Length and EAM Cover) were centred and scaled.

Model selection revealed that site and reef did not explain any variation in feeding rates across latitude, between seasons or across the continental shelf, and were subsequently removed from all analyses. All models were fit with a gamma error distribution with a log-link function. Weakly informative priors were used on all intercepts [~*Normal*(0, 10)], coefficients [~*Normal*(0, 2.5)], and shape [*Exponential*(rate=1)] with 5000 iterations, a warmup of 3000, 3 chains and a thinning factor of 5 for all models, with the exception in the cross shelf comparison of *N. unicornis* a thinning factor of 3 was used, and *C. striatus* a thinning factor of 2 to ensure effective sampling.

To analyse differences in the availability of preferred feeding substrata (cover of EAM and macroalgae) among latitudes and shelf positions, individual linear and generalized linear mixed effects models 'stan_glmer' were used. For the latitude comparison, models included latitude as a fixed factor and site as a random intercept to account for any variation between sites. For the seasonal comparison, season was included as a fixed factor and site as a random intercept. For the cross shelf comparison, shelf position was included as a fixed factor and site as a random intercept. All models were fit with a poisson distribution with a log-link function, with the exception of the models for the cover of EAM across latitude and season which were fit with a gaussian distribution. Weakly informative priors were used on all intercepts [~*Normal*(0, 10)] and coefficients [~*Normal*(0, 2.5)] with 5000 iterations, a warmup of 3000, 3 chains and a thinning factor of 5 for all models.

Where differences in feeding rates or algal cover among latitudes, seasons or across the shelf were detected, pairwise comparisons were conducted using the emmeans package (version 1.3.3: Lenth 2019). For all models, trace plots were used to ensure chains were well mixed and converged on a stable posterior, and all rhat values (measure of sampling efficiency) did not exceed 1.1 and the ratio of effective samples versus total samples was > 0.5.

2.3 Results

2.3.1 Feeding Rate

There was strong evidence for an effect of latitude on the feeding rates of *N. unicornis* and *S. doliatus* (100% probability) and moderate evidence for an effect of latitude on the feeding rates of *C. striatus* (94% probability) (Figures 2.2a, A1a, Table A2). Model predictions indicated the feeding rates (mean bites minute^{-1} [95% credible intervals]) of *N. unicornis* and

S. doliatus were 56% and 53% higher at the northern GBR sites (29.3°C: *N. unicornis*: 13.10 bites minute^{-1} [10.16, 16.20], *S. doliatus*: 17.36 bites minute^{-1} [11.94, 22.92]) compared to the southern GBR sites (26.6°C: *N. unicornis*: 8.31 bites minute^{-1} [6.29, 10.57], *S. doliatus*: 11.19 bites minute^{-1} [8.06, 15.85]) (Figure 2.2a, Figure A1a, Table A2). Feeding rates of *C. striatus* were 15% higher in the northern GBR (25.95 bites minute^{-1} [19.72, 32.39]) compared to the southern GBR (22.58 bites minute^{-1} [17.02, 28.16]).

There was strong evidence (100% probability) for an effect of season on the feeding rates of *N. unicornis* and *S. doliatus*, with feeding rates (mean bites minute^{-1} [95% credible intervals]) being 25% and 58% greater in the summer (29.3°C: *N. unicornis*: 14.5 bites minute^{-1} [11.43, 18.80], *S. doliatus*: 18.40 bites minute^{-1} [12.11, 24.30]) compared to the spring (27.1°C: *N. unicornis*: 11.60 bites minute^{-1} [8.83, 14.70], *S. doliatus*: 12.10 bites minute^{-1} [7.73, 16.20]), respectively (Figure 2.2b, Figure A1b, Table A3a,b). There was also moderate evidence of an effect of season on the feeding rate of *C. striatus*, with a 92% probability that feeding rates were 10% higher during the summer (27.90 bites minute^{-1} [24.80, 30.70]) versus the spring (25.40 bites minute^{-1} [23.10, 27.80]; Figure 2.2b, Figure A1b, Table A3c). There was no evidence for an effect of EAM cover (%) on the feeding rates of *S. doliatus* and *C. striatus* between seasons (Table A3b,c), but weak evidence for a negative relationship (slope = 0.9) between feeding rates of *N. unicornis* and EAM cover (Figure A2, Table A3a).

There was strong evidence for an effect (100% probability) of shelf position for the feeding rates of *N. unicornis* only, where feeding rates at the mid- (10.31 bites minute^{-1} [4.77, 17.20]) and outer-shelf reefs (9.44 bites minute^{-1} [4.01, 15.84]) were 180% and 160% higher than the feeding rates at the inshore sites (3.65 bites minute^{-1} [1.66, 6.51]; Figure 2.2c, Figure A1c, Table A4). The lower feeding rates on inner-shelf reefs corresponded with a greater

proportion of bites being taken from fleshy macroalgae on these inner-shelf reefs (0.62) compared to mid- and outer-shelf reefs (0.01, Figure A4). There was also moderate evidence (95% probability) of a relatively small increase (19%) in feeding rates of *C. striatus* between inner- (22.59 bites minute^{-1} [14.24, 32.57]) and mid-shelf sites (26.91 bites minute^{-1} [18.31, 38.47], Figures 2.2c, A1c, Table A4c).

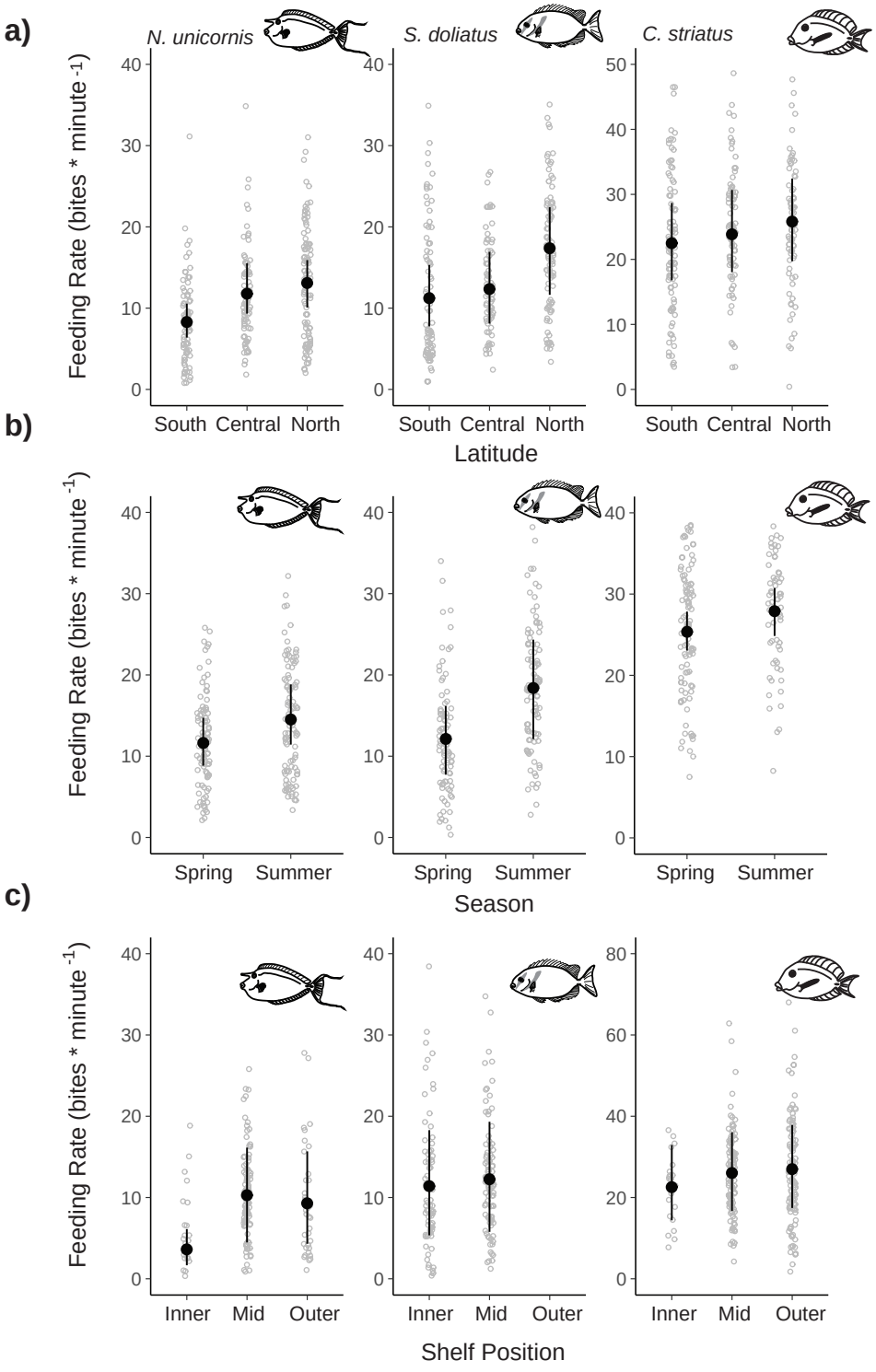

Figure 2.2: Comparison of feeding rates of three herbivorous fishes among (a) three latitudes on the GBR, (b) two seasons at the mid-shelf reefs in the northern GBR and (c) three continental shelf positions in the northern GBR. Filled circles are mean model estimates of Bayesian mixed effects models with gamma distributed errors, ± 95% Credible Intervals, open grey circles are partial residuals of the model.

2.3.2 Dietary Resource Availability

Across latitude, percent cover of EAM was highest at the low latitude reefs (61.0% [46.1.5, 75.7]) and decreased by 40% and 56% to the central (36.4% [22.6, 50.6]) and southern (26.9% [12.5, 42.5]) sites, respectively (Figures 2.3a, A3a, Table A5). Macroalgal cover was low (< 2%) and did not differ among latitudes (Figures 2.3a, A3a, Table A5). The cover of EAM and macroalgae was similar between seasons (Figures 2.3b, A3b, Table A6). Across the continental shelf, the cover of EAM was highest in the mid- (65.3% [59.6, 71.6]) and outer-shelf reefs (62.5% [56.9, 69.6]) and decreased by 78-79% in the inner-shelf (13.6% [11.7, 15.9]: Figure 2.3c, Figure A3c, Table A7). Macroalgal cover was highest at the inner-shelf, (75.5% [67.2, 83.5]) and decreased by 98-99% in the mid- and outer-shelf reefs respectively (Figures 2.3c, A3c, Table A7).

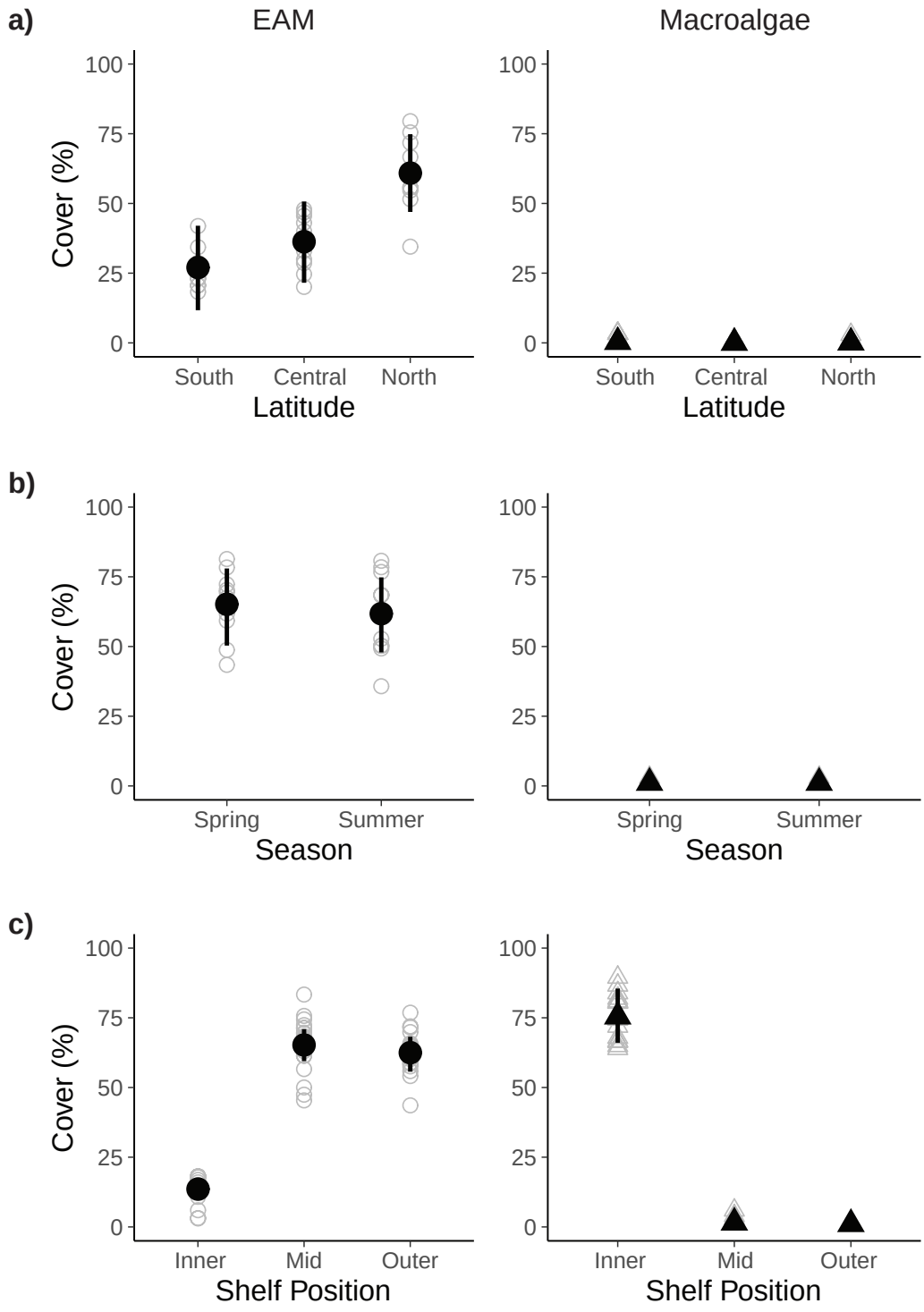

Figure 2.3: Comparison of the cover of EAM (circles) and macroalgae (triangles) among (a) three latitudes along the GBR, (b) two seasons in the low latitude sites of the GBR, and (c) across three shelf positions across the continental shelf in the northern GBR. Filled symbols are mean model estimates ± 95% Credible Intervals, and open symbols are partial residuals of the model, n=4 transects/site).

2.4 Discussion

Herbivory is a critical process in structuring algal communities on coral reefs (Hughes et al., 2007; Rasher et al., 2013). The majority of previous studies have focussed on how changes to herbivore population sizes affect benthic communities, but few consider the potential importance of environmental temperature to herbivory. The results of this study show that feeding rates of all three species with distinct diets were greater in the northern GBR compared to the southern and central GBR (when compared during the austral summer), and were also higher during summer versus spring (in the northern GBR). These results suggest that feeding rates increase with increasing temperature, at least over the range of temperatures to which fishes were exposed in this study. However, resources also influenced feeding, particularly for the macroalgal browser *N. unicornis*, where feeding rates decreased when there was a large increase (750%) in macroalgal cover, its preferred dietary resource. There was some variation in herbivorous fish assemblages among latitudes and shelf positions (Figure A7), however, this variation did not correlate with changes in feeding rates. While the magnitude of the effect of temperature varied between species, the consistency of the relationship between feeding rates and temperature suggests that temperature as an important influence on feeding rates of herbivorous fishes.

In the present study a temperature increase of 2-3°C across both spatial (i.e., latitude) and temporal (i.e., seasonal) scales resulted in elevated feeding rates of all three herbivorous species. The latitudinal trends in feeding cannot be attributed to temperature alone, as EAM cover also increased in the low latitude reefs. However, similar increases in feeding were observed from spring to summer in the northern GBR where EAM cover remained constant. Furthermore, a 7.5-fold increase of EAM cover from inner- to mid-shelf reefs did not correlate with increased feeding rates across the continental shelf, suggesting that the

latitudinal trends in feeding observed may more likely to be attributed to changes in temperature. Therefore, increases in feeding rates across latitude and between seasons were evident irrespective of the availability of their preferred feeding substrata. Specifically, I found a 25-56%, 53-58% and a 10-15% increase in feeding rates for *N. unicornis*, *S. doliatus* and *C. striatus* respectively in response to a 2-3°C increase in temperature across latitude and between seasons, presumably as increased temperature increases metabolic rate and energetic demand (Gillooly et al., 2001; Brown et al., 2004). These results are broadly consistent with previous studies that found increasing feeding rates with increasing temperature (e.g., Floeter et al., 2005), however, this study revealed changes in feeding rates over a relatively moderate temperature range (i.e. 2-3°C), which also resulted in a relatively smaller increase in feeding. Previous studies have found larger increases in feeding rates (up to a 5-fold increase) of subtropical and tropical herbivorous fishes (f. Acanthuridae, f. Siganidae, f. Labridae (Scarini), f. Pomacentridae), but under larger increases in temperature, i.e. across latitude (+9°C: Floeter et al., 2005), between seasons (summer vs. winter: +5-7°C: Carpenter, 1986; Polunin & Klumpp, 1992; Ferreira et al., 1998), and in upwelling versus non-upwelling environments (+8°C: Smith, 2008). However, these previous studies did not assess the potential role of dietary resource availability in influencing feeding. Therefore, it is unclear whether the differences in the magnitude of response between this study is driven by temperature alone, or the potential differences in dietary resources.

While the feeding rates of all three study species responded positively to increases in temperature, the magnitude of this response varied between species. The turf algal cropper *S. doliatus* was the most sensitive to temperature where a ~2-3°C increase resulted in a 53-58% increase in feeding rates, and the detritivore *C. striatus* was the most insensitive to temperature with only a 10-15% increase in feeding. While the differences in the magnitude

of the responses are difficult to resolve, they may be related to differences in the shape of individual thermal performance curves (Brown et al., 2004), the digestibility and nutrition of algal materials (Clements et al., 2009), or daily activity and energetic demands of the individual (Huey & Kingsolver, 2019). Detritus and diatoms, the dietary targets of *C. striatus* are higher in protein than the algal components within the EAM (Montgomery et al., 1989; Crossman et al., 2001) which may explain why the change feeding of *C. striatus* was less than that of *S. doliatus*, as *C. striatus* may be already obtaining enough energy to respond to increased metabolic demand. Furthermore this study indicates that *C. striatus* feeds at a relatively greater rate than *S. doliatus* and *N. unicornis* (~25-50%, Figure 2.2), but over a smaller area (*C. striatus* homerange:8-16m^2; Krone et al., 2008), therefore expending less energy foraging. Lastly, feeding may remain relatively unchanged as reduced activity is a behavioural mechanism to conserve energy at elevated temperatures, as shown for the predatory reef fish *Plectropomus leopardus* (Johansen et al., 2014; Scott et al., 2017). While the mechanisms explaining the differences in magnitude of response between the study species remain unclear, the consistent positive relationship between feeding across latitude and season suggest temperature as an important driver for herbivore feeding, but does not discount the importance of the quality and quantity of dietary resources.

Unlike temperature, the effect of dietary resource to feeding rates was not consistent among species. Macroalgal cover had a strong effect on the feeding of the macroalgal browser *N. unicornis*, across the continental shelf, where feeding decreased by 65% when there was a 750% increase in its preferred dietary resource. Sixty-two percent of total bites taken by *N. unicornis* were on canopy forming phaeophytes in the inner-shelf reefs, predominantly *Sargassum*, *Sargassopsis*, and *Hormophysa*: the preferred dietary items of *N. unicornis* (Choat et al., 2002; Hoey & Bellwood, 2009). The reduced feeding of *N. unicornis*

in response to increases in available macroalgae is likely due to greater yield per bite from large leathery and foliose phaeophytes versus small filamentous and corticated algae, and potentially gaining greater nutritional value. EAM cover had a relatively smaller effect on the feeding rates of *N. unicornis* where a 30% increase in EAM cover (within the mid-shelf reefs in the northern GBR) resulted in only a 20% decline in feeding rates. Increased resource availability reduces the search and detection time to locate a resource, and should therefore increase feeding for species that are resource/nutrient limited (Börger et al., 2008; Dell et al., 2014), such as herbivorous fishes. However, reductions in EAM cover are often correlated with increases in coral cover, and therefore protection against predators and competitors, potentially increasing feeding rate and frequency (Williams et al., 2001; Nash et al., 2012), which might explain the reduced feeding of *N. unicornis* in relation to EAM cover. Furthermore, an increase of 750% in EAM cover, the preferred feeding substrata for *C. striatus,* between the inshore and mid-shelf reefs resulted in only a small increase (10%) in feeding of the detritivore *C. striatus.* The protein content of detritus, the dietary target of *C. striatus,* decreases across the continental shelf towards the outer reefs in the northern GBR (Crossman et al., 2001). Therefore it could be likely that potential changes to the quality and quantity of detritus within the EAM may be driving changes to the feeding rates of *C. striatus* between the inner and mid-shelf reefs. The turf algal cropper *S. doliatus* was relatively insensitive to changes in EAM cover across latitudes, between seasons and across the continental shelf, potentially due to its cosmopolitan diet and the wide range of targeted dietary resources within the EAM (red and green filamentous and foliose algae and brown foliose macroalgae: Choat et al. 2002; Hoey et al. 2013). Nutrition and productivity of resources are also important drivers for herbivorous fish foraging behaviour, abundance and demographics (Ford, 1983; Choat & Clements, 1998; Russ, 2003; Johnson et al., 2019), and cannot be inferred by percent cover. However increases in the abundance of available grazing

substrata could potentially offset a nutritionally poor resource or increase the likelihood of finding a nutritionally rich resource.

This study shows that relatively small increases in temperature lead to increases feeding rates of three herbivorous fish species, although the magnitude of the effect was species-specific. This positive relationship between feeding and temperature may mean that herbivores could keep pace with predicted increases in algal cover under future warming. However, as herbivores are nutrient limited, it is unclear whether they will be able to compensate for increased metabolic demand under future increases in temperature through increased feeding rates alone, or whether they may have to result to alternate strategies such as reduced activity (e.g. Johansen et al. 2014; Scott et al. 2017), or feeding selectivity (Lemoine et al., 2013). Furthermore, as SSTs continue to increase, the higher latitude range of many tropical herbivores has already been shown to increase, leading to the tropicalization of fish communities in subtropical/temperate zones (Basford et al. 2016; Vergés et al. 2014, 2016), the deforestation of kelp forests, and the transition to turf-dominated habitats (Bennet et al. 2015; Filbee-Dexter & Wernberg, 2018). As such, any behavioural changes of herbivores may have implications for top down control of algal biomass, and potentially future ecosystem structure of coral reefs and tropical-subtropical transition zones. However, to fully understand the net effect of temperature to herbivory, it is also important to consider the effect of temperature on resources themselves, and importantly, the relative rates of consumer pressure versus resource productivity (Bruno et al., 2015).

Chapter 3: Temperature-driven trophic mismatch between the production and consumption of algal turfs on coral reefs[2]

3.1 Introduction

Interactions between primary producers and primary consumers (i.e., herbivores) are fundamental in structuring plant communities of marine and terrestrial ecosystems (Lubchenco & Gaines, 1981; Carpenter, 1986; Huntly, 1991; Duffy & Hay, 2001; Ohgushi, 2005). Variation in herbivory can influence the biomass, composition and productivity of local plant communities (Cyr & Face, 1993; McNaughton et al., 1989), with areas of intense herbivory being characterised by a low biomass of highly productive herbaceous plants, while areas of low herbivory are typically characterized by a high biomass of less productive woody plants in terrestrial systems (e.g. Dublin et al. 1990; Dobson and Crawley 1994), or leathery macroalgae in marine systems (e.g. Hughes et al. 2007). To date, the vast majority studies have used the abundance of herbivores as a proxy for feeding intensity when investigating the influence of herbivory on plant communities (Lubchenco & Gaines, 1981; McNaughton et al., 1989; Cyr & Face, 1993; Olff & Ritchie, 1998), however, other environmental factors that influence rates of production and/or consumption of primary producers could also influence plant community biomass and composition (Bruno et al., 2015). Environmental temperature determines the rates of biological processes (e.g. metabolism, growth) for ectotherms and influences rates of growth and production of plants and algae (Huey & Stevenson, 1979). Therefore, changes in environmental temperature may alter the biomass and composition of primary producers if primary production and consumption by herbivores differ in their thermal sensitivity (O'Connor et al., 2011; Bruno et al., 2015). As environmental temperatures are increasing globally (Bindoff et al., 2019),

[2] Graba-Landry, A., Loffler, Z., Pratchett, M. S., Hoey, A. S. Temperature-driven trophic mismatch between production and consumption of algal turfs on coral reefs. (*In Prep)*

understanding how temperature may influence the outcomes of plant-herbivore interactions is key to predicting the future configuration of both terrestrial and aquatic ecosystems (Dell et al., 2014; Bruno et al., 2015; Nagelkerken & Munday, 2016; Gordon & Letnic, 2019).

The effect of increasing temperature to the outcome of plant-herbivore interactions is dependent on the effects of temperature to both plant production and the metabolic demands of herbivores, and hence their consumption of plant material (O'Connor, 2009; O'Connor et al., 2011; Bruno et al., 2015). Within a species' thermal tolerance range, rates of biological processes (i.e. metabolism, growth) increase exponentially with increasing temperature until a thermal optimum is reached, after which performance rapidly declines (Huey & Stevenson, 1979; Brown et al., 2004). Differences in responses of consumers and producers to changing temperature can lead to a trophic mismatch where consumption exceeds production, or vice-versa (Dell et al., 2014). The direction of this mismatch is dependent on how close producers and consumers are to their thermal optima and the rate at which they approach their thermal optima (Dell et al., 2014). As cellular respiration is more sensitive to temperature than photosynthesis, plants and algae have been suggested to be more robust to temperature than their consumers (Allen et al., 2005; López-Urrutia et al., 2006). Indeed, algal consumption by invertebrate herbivores in temperate marine systems has been shown to be more sensitive to increases in temperature than the production of algae or phytoplankton, with feeding rates exceeding production following small increases in temperature (O'Connor, 2009; O'Connor et al., 2009; Mertens et al., 2015). However, should the temperature increase exceed the thermal optimum for herbivores, consumption may crash, providing a refuge for producers (Mertens et al., 2015). How algal consumption and production are affected by changing temperature in tropical systems is less understood. Tropical ectotherms (and plants and algae) have evolved under relatively stable thermal environments, and typically have a narrow

thermal tolerance range, reduced thermal safety margin, with many living at or near their thermal optima (Tewksbury et al., 2008; Sunday et al., 2012). Consequently, tropical ectotherms are generally more sensitive to small temperature increases than temperate species. Understanding how tropical algal production and consumption respond to changing temperature will be key to predicting the future structure of these ecosystems.

Tropical coral reefs are one of the ecosystems most threatened by anthropogenic climate change (Walther et al., 2002; Hughes et al., 2017). The increased frequency and intensity of marine heatwaves have resulted in recurrent mass coral bleaching events, leading to a global decline in coral cover (Hughes et al., 2017a, 2018a,b), and concurrent increases in turf- and macro-algal cover that rapidly colonise the dead coral skeletons (Diaz-Pulido & McCook, 2002; Hughes et al., 2018; Leggat et al., 2019). The recovery of coral assemblages is dependent, at least to some extent, on the feeding activities of grazing fishes that maintain algal assemblages in a cropped state of productive turfs and prevent the establishment of fleshy macroalgae that compete with corals for benthic space (Hughes et al., 2007; Rasher et al., 2013). The balance between the production of algae, and its consumption may be disrupted under warming, as fish and algae have different thermal requirements (López-Urrutia et al., 2006; Bruno et al., 2015). While several studies have related spatial and/or temporal variation in feeding rates of herbivorous fishes to temperature (e.g. Polunin & Klumpp, 1992; Ferreira et al., 1998; Floeter et al., 2005; Smith 2008; Afeworki et al., 2013) or algal production (e.g. Klumpp & McKinnon, 1989; Ferrari et al., 2012), the relationship between temperature and feeding rates and algal growth on coral reefs are yet to be considered.

The aim of this study was to quantify seasonal variation in the growth of algal turfs and the feeding rates of grazing herbivorous fishes on coral reefs, and in doing so, assess the potential for a temperature-driven trophic mismatch. I hypothesized that turf growth would be less sensitive to changes in temperature than herbivore feeding rates, as photosynthesis is less constrained by temperature than cellular respiration (López-Urrutia et al., 2006). If feeding activities of herbivorous fishes are increasingly constrained at higher temperatures, sustained increases in ocean temperatures may allow algal productivity to exceed the regulatory capacity of herbivorous fishes, especially during summer.

3.2 Methods

3.2.1 Study Sites

This study was conducted on coral reefs surrounding Lizard Island in the northern Great Barrier Reef (14°40’43.842” S, 145°26’52.2924” E, Figure 3.1). Lizard Island is a high island located approximately 30 km from the north Queensland mainland coast. The production and consumption of algal turfs, the predominant feeding substratum of grazing fishes, were quantified on three reef crest sites exposed to prevailing SE trade winds (Figure 3.1) in each of four seasons: spring (October – November 2017), summer (January – February 2018), autumn (April – May 2018) and winter (July 2018). The reef crest was selected as herbivore abundance, biomass and diversity, and rates of algal production and consumption are generally highest within this habitat (e.g., Russ, 2003, Hoey & Bellwood, 2010). Sea surface temperature data within each sampling period was sourced from the Integrated Marine Observing System (IMOS) maintained by the Australian Institute of Marine Science weather station at Lizard Island (AIMS, 2018).

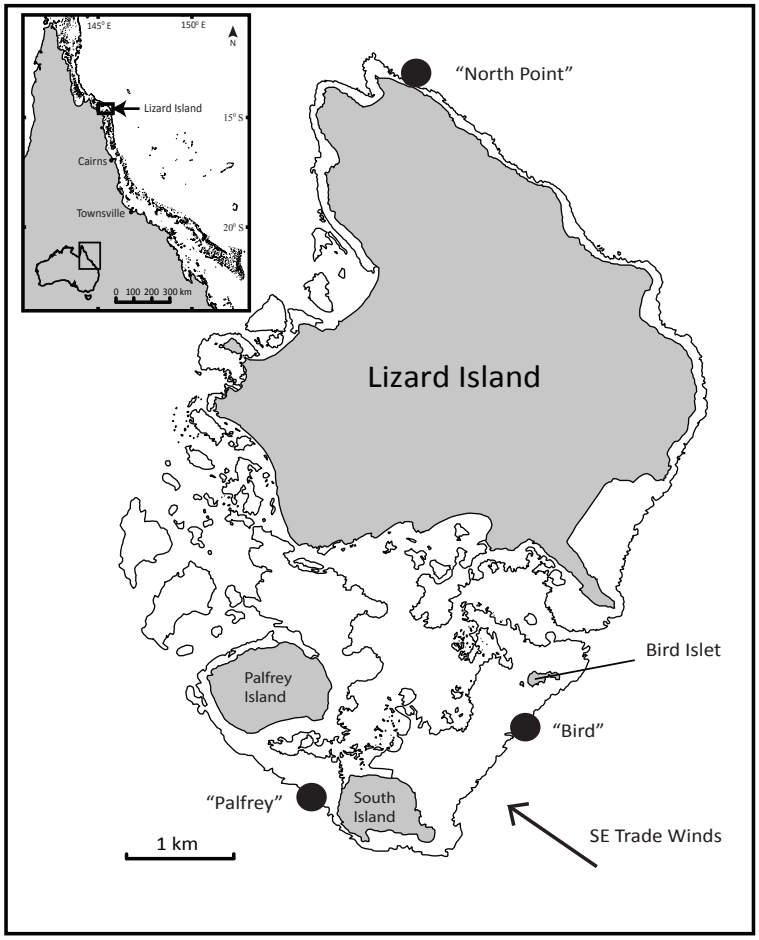

Figure 3.1: Map of showing the location of Lizard Island in relation to Australia and the Great Barrier Reef (inset) and the location of the three exposed reef crest study sites around the Lizard Island Group.

3.2.2 Turf algae growth

The growth of turf algae was quantified as the rate of accumulation of biomass (g DW day^{-1}) of turf algal communities grown on terracotta settlement tiles in the absence of herbivory by grazing fishes. Ten terracotta tiles (10 x 10 x 0.5cm) were secured to the reef substratum at each site in each season using a stainless steel baseplate and push-mount system (following Mundy, 2000; Trapon et al., 2013). Tiles were initially deployed at each site for a minimum of 2 months to allow turf algal and microbial assemblages to develop (Russ, 1987). At the start of each algal growth period the tiles were removed from the base plates, lightly scraped with a paint scraper to remove algal biomass, and re-attached to the reef. Individual mesh

cages (4,000cm^3, 1 cm^2 plastic mesh) were secured over each tile to exclude feeding on the tiles by large herbivorous fishes, and did not shade the tiles significantly. After three-weeks, tiles were collected and transported to the laboratory, and lightly rinsed under running seawater to remove sediment and any loose organic matter. Algal biomass was then removed from the upper surface of the tile using a paint scraper and dried in an oven (60°C) to constant weight (72 hours). The dry weight was measured using an analytical balance (0.0001g).

3.2.3 Herbivore feeding rates

This study used two complimentary methods to assess seasonal changes to feeding on turf algae substrata: focal feeding observations to assess species-level changes feeding rates, and video analysis of local fish assemblages feeding on the reef benthos to assess assemblage-level changes in feeding rates. Feeding rates of eight locally-abundant nominally herbivorous surgeonfish (f. Acanthuridae) and rabbitfish (f. Siganidae) species were quantified at each site in each of four seasons. The eight species selected encompassed a range of feeding modes and diets (i.e, algal croppers: *Siganus doliatus* (Guérin-Méneville 1829-38) , *Siganus corallinus* (Valenciennes 1835), *Acanthurus nigrofuscus* (Forsskål 1775), *Zebrasoma scopas* (Cuvier 1829), *Zebrasoma velliferum* (Bloch 1795); detritivores: *Acanthurus olivaceous* (Bloch & Schneider, 1801), *Ctenochaetus striatus* (Quoy & Gaimard, 1825); browser: *Naso unicornis* (Forsskål 1775); Table B1) and all typically feed on algal turf covered substrata at Lizard Island.

Feeding rates of a minimum of 30 individuals for each of the eight species at each of the three sites in each season were quantified. An individual fish of a target species was haphazardly selected and its body length (total length, TL) estimated to the nearest

centimetre. After a 30 second acclimation period, each individual was followed for 3 minutes during which the number of bites and the feeding substratum were recorded. Three minutes was chosen as it would encompass multiple foray events (Kelly et al., 2017) and has been used extensively to quantify feeding rates of coral reef fishes (Berumen et al., 2005; Pratchett, 2005; Keith et al., 2018; Robinson et al., 2020), including herbivorous species (Kelly et al., 2017; Hoey, 2018; Robinson et al., 2020). If the focal fish displayed any altered behaviour due to diver presence, the observation for that individual was terminated. Care was taken not to re-survey the same individual by noting specific markings and size of fishes, and observers moved in one direction along the reef between consecutive observations (Keith et al., 2018). To standardize fish sizing across observers, all observers estimated the length of pieces of PVC of known length placed along the reef crest prior to commencing feeding observations, and self-assessed until estimates were within one centimetre of the known length.

Grazing pressure by local herbivorous fish assemblages was quantified within replicate 1 m^2 quadrats on the reef crest at each site in each season. Areas with high cover of turf algae (>80%) and low cover of live coral (<10%) were haphazardly selected and filmed using small stationary cameras (GoPro) at each site, in each season. A 1 m^2 quadrat was placed on the reef substratum and filmed for approximately one minute to demarcate a $1m^2$ area. A 30 cm ruler was held adjacent to each corner of the quadrat for ~10 s at the start of each video to provide a scale to estimate the total length (TL, cm) of fish in the footage at different areas within the quadrat. Due to battery failure and camera fogging a total of 6-9 replicate 1hr videos were analysed per site per season, with the exception of “Bird” in the Autumn, which only had three replicates. Video observations were conducted between 9 am to 3 pm to minimise diel variation in feeding rates of herbivorous fishes

(Zemke-White et al., 2002) and during mid to high tides to reduce the influence of water depth on feeding. The entire video footage was viewed and for any fish observed taking bites from the substratum within the quadrat the species, total length (cm), and number of bites were recorded.

3.2.4 Turf algae cover, benthic composition, and herbivorous fish assemblages

To account for the potential influence of dietary resource (algal) availability, or herbivore competition for resources, I quantified the benthic and herbivore assemblages at each site in each season. Herbivorous fish assemblages and benthic composition were quantified along four replicate 50 m transects at each site, during each season. An observer (always AGL) recorded the species and total length of all roving nominally herbivorous fishes (including detritivores) > 10 cm TL within a 5m wide belt while simultaneously deploying the transect tape (following Hoey et al. 2011). Care was taken not to resurvey fish that left and subsequently re-entered the transect area. Adjacent transects were separated by a minimum of 10 m. The benthos directly under the transect tape was recorded every 0.5 m. Benthic categories were recorded as turf algae, live hard coral, soft coral, macroalgae, crustose coralline algae, sessile benthic invertebrates, sand, or rubble. I quantified the cover of turf algae among sites to account for the potential influence of resource availability on herbivore feeding rates.

3.2.5 Statistical Analysis

Bayesian generalized linear mixed models were used to analyse differences in turf algal growth, turf algae cover, feeding intensity of herbivorous fish assemblages and individual feeding rates of the eight study species. All analyses were conducted using R (version 3.5.2: R Development Core Team 2016). Markov chain Monte Carlo sampling (Carpenter et al.,

2017) were used to fit models in STAN (Stan Development Team, 2018) using the rstanarm package (version 2.17.4: Goodrich et al., 2018). The tidybayes (version 1.0.4: Kay 2019), broom (version 0.5.1: Robinson & Hayes, 2018) and coda (version: 0.19.2: Plummer et al., 2006) packages were used to summarise model outputs using highest posterior density (HPD) intervals with a probability of 95%. Model selection was conducted by comparing Leave One Out Information Criterion values (Vehtari et al., 2017). Collinearity between fixed factors was assessed using the 'vif' function using the car package (version 3.0.4: Fox & Weisberg, 2019). Where differences in turf algae growth, turf algae cover or fish feeding rates were detected, pairwise comparisons were conducted using the emmeans package (version 1.3.3: Lenth, 2019). Strong evidence for an effect was determined if 95% HPD credible intervals did not cross 0 for gaussian models, or 1 for back-transformed non-gaussian models. Plots were produced using ggplot2 within the tidyverse package (version 1.2.1: Wickham, 2016).

To analyse differences in turf algal growth on terra cotta tiles between seasons, a generalized linear mixed effects model 'stan_glmer' was used. The model included Season (spring, summer, autumn and winter), as a fixed factor, and individual tile as a random intercept in the model as each individual tile was resurveyed each season. Site did not explain any variation in growth, and was subsequently excluded from the analysis. The model was fit with a gamma error distribution with a log-link function. Weakly informative priors were used on all intercepts [~*Normal*(0, 10)], coefficients [~*Normal*(0, 2.5)], and shape [*Exponential*(rate=0.1)] with 5000 iterations, a warmup of 1000, 3 chains and a thinning factor of 3.

To analyse differences in the feeding rates of herbivore assemblages, a linear model 'stan_glm' was used. The model included Season as a fixed factor. As Site did not explain

any variation in assemblage feeding rates, it was excluded from the analysis. The model was fit with a gaussian error distribution with an identity function. Normality and homogeneity of variance was assessed with Q-Q and box plots. Weakly informative priors were used on all intercepts [~*Normal*(0, 10)], coefficients [~*Normal*(0, 2.5)], and sigma[~*Exponential*(rate=1)] with 5000 iterations, a warmup of 1000, 3 chains and a thinning factor of 3.

To analyse differences in individual feeding rate between seasons and differences in turf algae cover individual generalized linear mixed effects models 'stan_glmer' were used for each fish species. The models included Season, Total Length (to account for any effect of body size; centred and scaled), and turf algae cover (to account for any effect of resource availability; centred and scaled) as fixed factors, and observer as a random intercept in the model to account for variation between observers. Site did not explain any variation in feeding rates and was excluded from the analyses. All feeding rate models were fit with a gamma error distribution with a log-link function. Weakly informative priors were used on all intercepts [~*Normal*(0, 10)], coefficients [~*Normal*(0, 2.5)], and shape [*Exponential*(rate=1)] with 5000 iterations, a warmup of 3000, 3 chains and a thinning factor of 5 for all models.

To analyse differences in turf algae cover between sites, a linear model 'stan_glm' was used. The model included Site as a fixed factor. The model was fit with a gaussian error distribution with an identity function. Normality and homogeneity of variance was assessed with Q-Q and box plots. Weakly informative priors were used on all intercepts [~*Normal*(0, 10)], and coefficients [~*Normal*(0, 2.5)], with 2000 iterations, a warmup of 500, 3 chains and a thinning factor of 3.

For all models, trace plots were examined to ensure chains were well mixed and converged on a stable posterior, and all rhat values (measure of sampling efficiency) did not exceed 1.1 and the ratio of effective samples versus total samples was > 50%. Priors were determined to be weakly informative from diagnostic plots showing that the median and central intervals between posterior and prior were sufficiently wide, without being flat.

To visualise any variation in herbivorous fish assemblages or benthic communities among sites or seasons individual non-metric Multi-Dimensional Scaling (nMDS) analysis were performed using the "vegan" package in R (Oksanen et al., 2019). The analysis was based on Bray-Curtis similarities, using a double Wisconsin standardization on square-root transformed data. Individual PERMANOVAs were conducted to determine if there were differences in fish and benthic communities across seasons and sites.

3.3 Results

Mean monthly sea surface temperatures at Lizard Island varied approximately 5°C over the 12 months of this study, from 24.08°C ± 0.03 SE in July 2018 to 29.05°C ± 0.14 SE in February 2018 (Figure 3.2a,b). Mean temperatures during the seasonal sampling periods were 27.17°C ± 0.07 SE in spring, 28.9°C ± 0.06 SE in summer, 26.9°C ± 0.03 SE in autumn, and 24.08°C ± 0.04 SE in winter (Figure 3.2a, b; AIMS, 2018).

3.3.1 Turf algae growth

There was strong evidence (100% probability) of an effect of season on the growth of turf algae on terra cotta tiles (Figure 3.2b, Table B2). Model predictions suggested that growth (mean g day^{-1} [95% credible intervals]) in the summer (0.09 g day^{-1} [0.08, 0.10]) was 59%, 46% and 30% lower than in the autumn (0.15 g day^{-1} [0.13, 0.16]), spring (0.13 g day^{-1} [0.12,

0.15]) and winter (0.119 g day^{-1} [0.11, 0.13]) respectively (Figure 3.2a). Growth was also 22% lower in the winter versus autumn (Figure 3.2a).

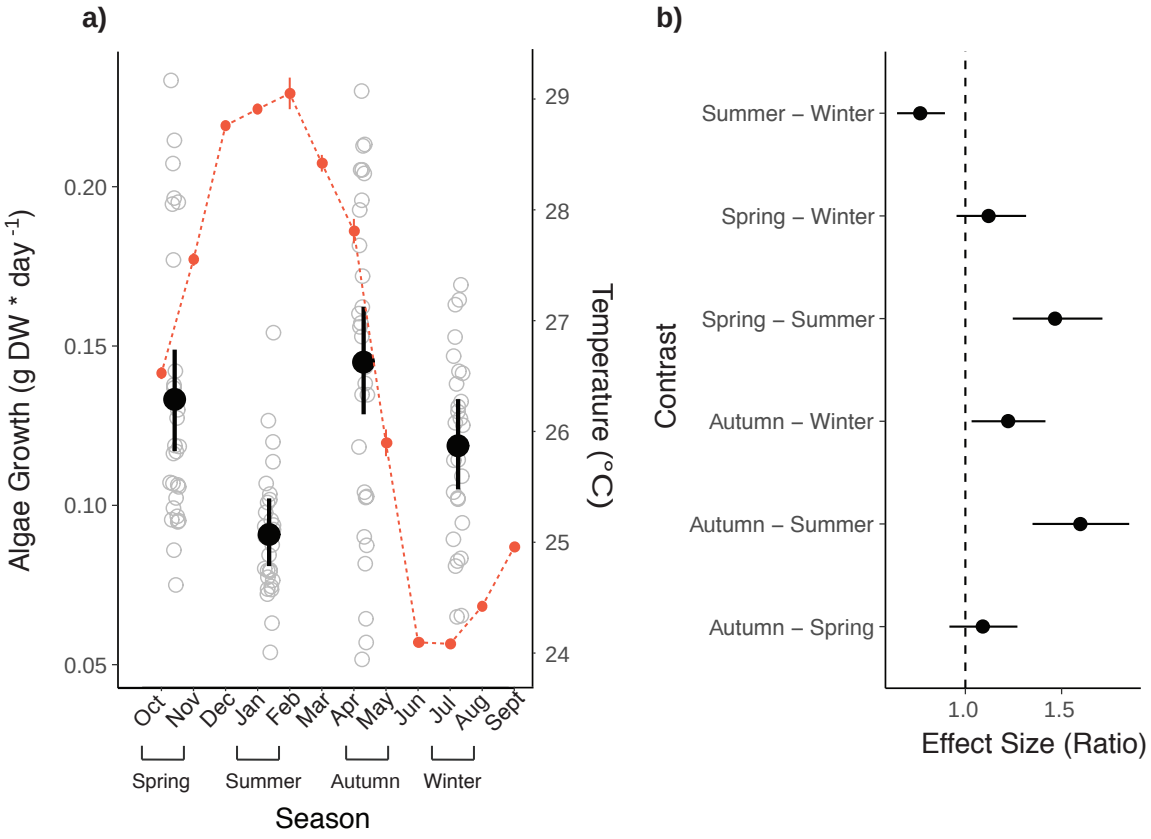

Figure 3.2: a) Seasonal variation in the growth of turf algae growth at three reef crest sites around Lizard Island. Model estimates are back-transformed to the natural scale using a log link function. Mean monthly sea surface temperatures (°C) at 8.8m ± SE are indicated in red. Filled circles and lines are mean model estimates ± 95% credible intervals and grey open circles are model residuals. b) The effect sizes for pairwise comparisons of turf algae growth for each season. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that turf algae growth is greater in the season that is first listed (to the right of the line) or second listed (to the left of the line).

3.3.2 Individual Herbivore Feeding Rates

There was strong evidence (100% probability) of an effect of season on the individual feeding rates of all eight herbivore species, with feeding rates 56% (*Z. velliferum*) – 118% (*N. unicornis*) higher in the summer compared winter (Figures 3.3, B1, Tables B3-B10). Feeding rates (mean bites minute^{-1} [95% credible intervals]) were generally similar between spring and summer (*N. unicornis*, *A. olivaceus, Z. velliferum*) or spring, summer and autumn (*C. striatus, Z. scopas*, *A. nigrofuscus*, and *S. doliatus*) (Figures 3.3, B1, Tables B3-B9). The only exception was *S. corallinus,* whose feeding rate was the greatest in the summer (18.33 bites minute^{-1} [15.60, 21.80]), compared to autumn (14.05 bites minute^{-1} [11.82, 16.60]) and spring (13.78 bites minute^{-1} [11.54, 16.40]; Figures 3.3h, B1h, Table B10). There was also evidence for a relatively weak relationship between turf algae cover and feeding rates of two out of the eight species, *Zebrasoma velliferum* and *Zebrasoma scopas* (Figure B3, Tables B6-B7).

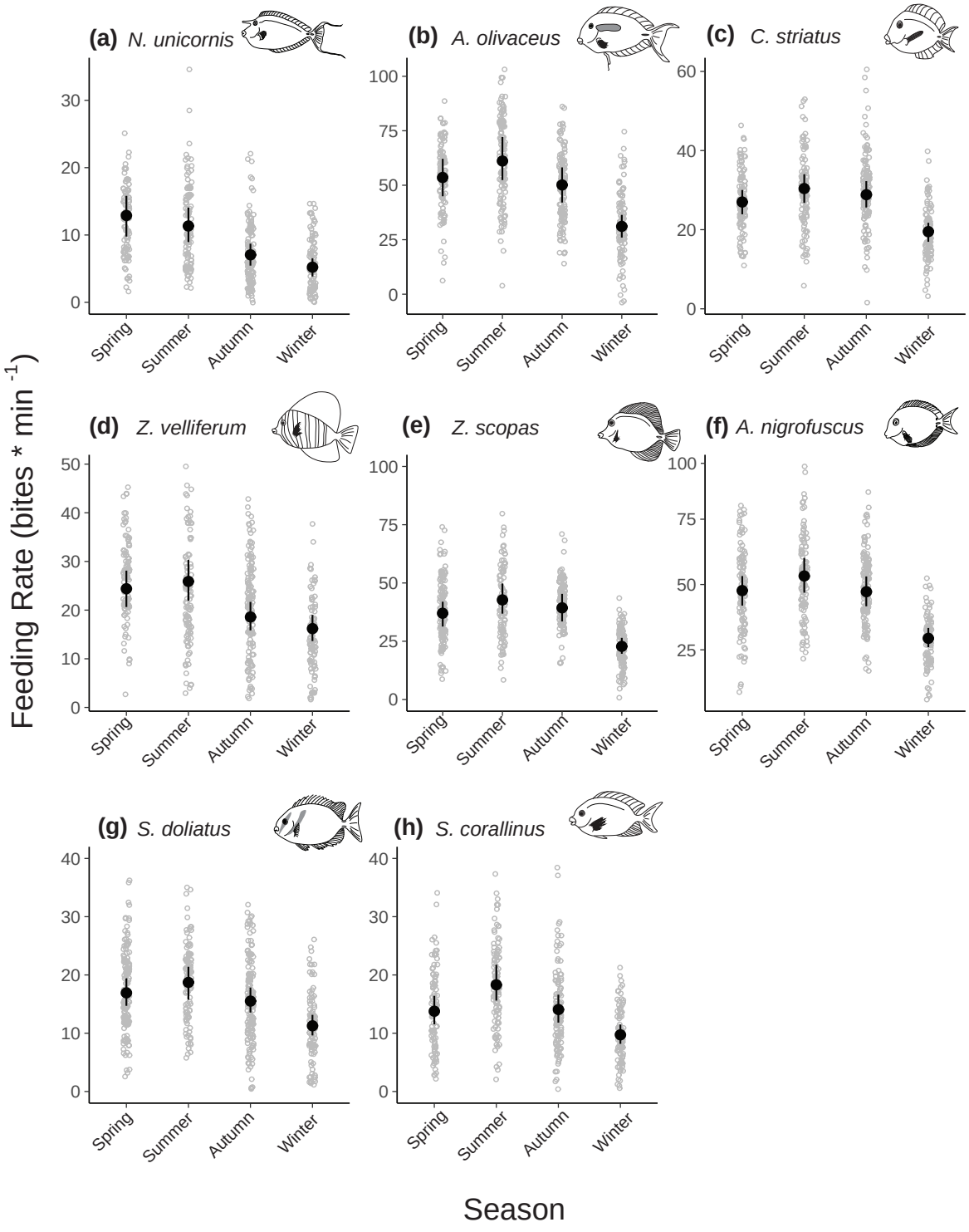

Figure 3.3: Seasonal variation in feeding rates (Bites minute^{-1}) of eight herbivorous fishes across four seasons on the reef crest at Lizard Island. Filled circles are estimated means of Bayesian mixed effects models with gamma distributed errors ± 95% credible intervals, open grey circles are partial residuals of the model.

3.3.3 Herbivore Assemblage Feeding Pressure

There was strong evidence for an effect of season on the feeding intensity of the local herbivorous fish assemblages on 1 m^2 of benthic substrata (Figure 3.4, Table B11). Model predictions suggest that assemblage feeding rates (mean bites $hour^{-1}$ m^{-2} [95% credible intervals]) were highest in the summer (535.0 bites $hour^{-1}$ m^{-2} [361.0, 730.0]) and lowest in the autumn (180.0 bites $hour^{-1}$ m^{-2} [103.0, 288.0]). There was a 99.9% - 99.6% probability that assemblage feeding rates in the winter (252.0 bites $hour^{-1}$ m^{-2} [156.0, 377.0]) and autumn were 53% and 76% lower than in the summer respectively. *Ctenochaetus striatus* (41.2%), *Acanthurus nigrofuscus* (25.0%), *Acanthurus lineatus* (14.9%) accounted for the majority of the total bites taken from the herbivorous fish community across all sites and all seasons.

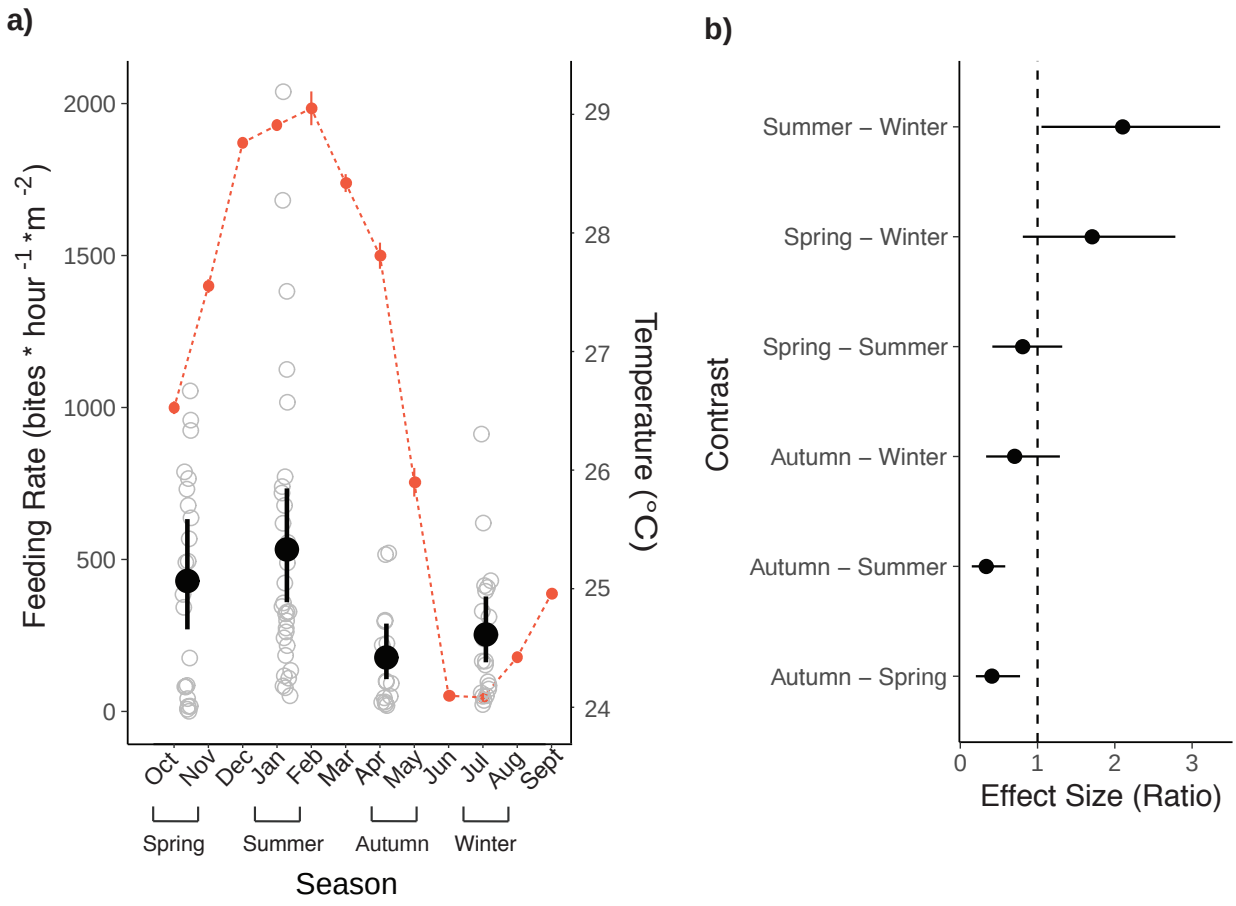

Figure 3.4: a) Seasonal variation in feeding rates of local herbivore assemblages (bites hour^{-1}) on 1m^2 benthic substrata with <10% coral cover at three reef crest sites around Lizard Island (Autumn (n=15, Spring (n=22), Summer (n=30), Winter (n=20)). Model estimates are back-transformed to the natural scale using a log link function. Mean monthly sea surface temperatures (°C) at 8.8m ± SE are indicated in red. Filled circles and lines are mean model estimates ± 95% credible intervals and grey open circles are model residuals. b) The effect sizes for pairwise comparisons of feeding rates of the local herbivore assemblage for each season. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that feeding rate is greater in the season that is first listed (to the right of the line) or second listed (to the left of the line).

Herbivorous fish and benthic assemblages

Differences in herbivorous fish assemblages among seasons were not consistent among sites (Figure 3.5a, Table B13, PERMANOVA: $F_{6, 46}$ = 1.7801, p=0.001). Differences in fish communities of North Point were driven largely by the presence of *Naso lituratus, Scarus altipinnus, Bolbometopon muricatum, Hipposcarus longiceps* which were absent at the other two sites (Figure 3.5a). Benthic communities also exhibited an interaction between season and site, driven by marked increase in cyanobacteria at one site Bird in the spring, and at Palfrey in the winter, and an increase in macroalgae (predominantly *Sargassum* spp.) in the summer at North Point (Figure 3.5b, Table B13, PERMANOVA, $F_{6, 46}$ =2.1502, p=0.001).

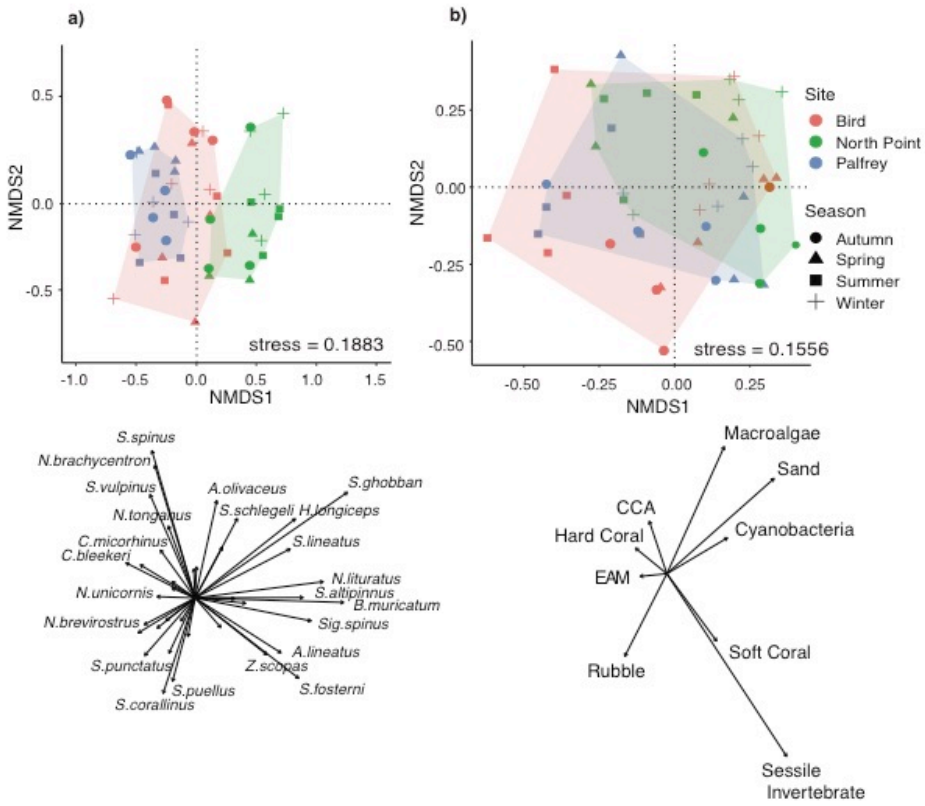

Figure 3.5: Multidimensional scaling analysis showing the relationship between a) fish communities, and b) benthic communities across three sites around Lizard Island. Results are based on Bray-Curtis similarities of Wisconsin double standardized and square-root transformed data. Vectors represent partial regression coefficients of the original variables (fish species, or benthic categories) within the two dimensions.

3.4 Discussion

Environmental temperature is a potentially important, yet often overlooked factor influencing the intensity and outcome of trophic interactions. Here, I found seasonal differences in feeding rates of herbivorous fishes (for both individual species and assemblages), and the growth of algal turfs, that were most likely related to changes in temperature. Feeding rates of herbivorous fishes were lowest in the winter (22-23°C) and highest in the spring and/or summer (27-29°C). The ubiquity of these changes across eight herbivorous fish species with varied diets, coupled with the lack of an effect of resource availability (except for *Z. velliferum* and *Z. scopas*), benthic communities or local herbivore communities (Figure 3.5) suggest environmental temperature was the most likely contributor to the observed changes in feeding rates. In contrast to herbivore feeding, turf algal growth was highest in the autumn/spring (27°C), and declined in both the summer (29°C) and winter (22-23°C) suggesting that algal growth may have a lower thermal optimum than herbivore feeding rates. Such differences in the responses of herbivore feeding rates and algae growth to temperature may lead to a trophic mismatch, and potentially strengthening fish-algae interactions in favour of fish consumption under elevated temperatures.

Processes driven by photosynthesis are predicted to be less sensitive to temperature than processes driven by cellular respiration (López-Urrutia et al., 2006). The results of this study suggest the opposite, with a peak in algal growth in the spring and autumn (27°C), and an overall increase in fish feeding rates from winter (23°C) to summer (29°C). These results are consistent with previous work on algal turfs which estimated biomass accumulation to be lowest in the winter and summer on the reef crest in the northern Great Barrier Reef (Klumpp & McKinnon, 1989), and increases in feeding rates of herbivorous fishes between winter and summer seasons (f. Acanthuridae and f. Labridae (Scarini) Carpenter, 1986; Polunin &

Klumpp, 1992; Ferreira et al. 1998). The general decline in algal growth in the summer, coupled with the general increase in feeding rates of all eight species in this study may limit the persistence of turf algae into the future, and may lead to resource limitation for consumers. This is in contrast to a trophic mismatch in a temperate intertidal marine system, where rates of production of filamentous and small thallate algae exceeded rates of consumption of snails at elevated temperatures, offering a potential herbivory-free thermal refuge for algae under warming, presumably as temperate intertidal environments experience extreme differences in temperature (Mertens et al., 2015). Therefore, the direction and magnitude of temperature driven trophic mismatches are context dependant, and depend largely on the thermal variability within the current local environment, which dictates how close producers and consumers are to their thermal optima and the rate at which they approach their thermal optima (Dell et al., 2014).

While algal growth peaked at a lower temperature than fish feeding rate, feeding rates were more sensitive to small increases in temperature than algal growth. For example, individual feeding rates were on average 82% (±7% SE) greater in the summer versus autumn, while turf algae growth was only 56% greater in autumn versus the summer. Such a change in relative rates in response between feeding and algal growth may further strengthen top down control within this trophic mismatch at elevated temperatures, therefore increasing the chance of dietary resource limitation for consumers. A similar response has been reported in a temperate pelagic marine system where consumption rates of zooplankton exceeded production, leading to a reduction in phytoplankton biomass, and potential resource limitation for consumers (O'Connor et al., 2009). The potential turf algae limitation on coral reefs may be offset by the increase in algal abundance over a greater area following coral bleaching events, and mortality (Hughes et al., 2018b; Leggat et al., 2019). However, community

grazing pressure is dependent on herbivore abundance, which is also predicted to increase with subsequent increases in turf algae abundance (Gilmour et al., 2013; Russ et al., 2018). Therefore the increased grazing pressure observed in this study, coupled with reduced algal growth at current summer temperatures, suggest that turf algal persistence and proliferation into the future may be less likely than previously assumed.

The results of this study suggest that temperature is the most likely contributor to the observed changes in feeding rates of herbivorous fishes. This data corresponds with previous studies which have also reported increases of 25-188% in individual feeding rates of herbivorous fishes under large increases in temperature; i.e. between winter and summer (~5-7°C difference in temperature: *Acanthurus lineatus*: Polunin & Klumpp, 1992), *Acanthurus bahanius*: Ferreira et al., 1998), in upwelling areas versus non-upwelling environments (+8°C, *Scarus ghobban*: Smith, 2008) and across latitude (+9°C, *Acanthurus bahanius*: Floeter et al., 2005). However, previous studies investigating the potential role of temperature in influencing herbivorous fish feeding are limited to one or two species, and do not also consider the potential for resource availability in influencing feeding, which makes inferring the role of temperature alone difficult. The consistency in response to seasonal variation in temperature in this study across eight herbivorous fish species with distinct dietary targets, coupled with the lack of effect of turf algae availability (except for *Z. velliferum* and *Z. scopas*), or changes to both herbivore and benthic communities across site and season (Figure 3.5, Table B13) suggest that environmental temperature was the most likely driver to changes in feeding rates. Furthermore, the response to temperature of grazing pressure at the assemblage level was broadly consistent with individual feeding rates with feeding increasing in the spring and summer, likely to compensate for increased metabolic demand (Brown et al., 2004). This is in contrast with feeding rates of adult parrotfish (*Scarus ferrugineus*) in the

Red Sea, where feeding rates decline past 32°C in the summer, presumably as they have exceeded their thermal optima (Afeworki et al., 2013). Reduced feeding and activity have also been reported in coral trout *Plectropomus leopardus* at summer maximum temperatures as a mechanism to conserve energy for increased metabolic demand (Johansen et al., 2014; Scott et al., 2017). While the herbivorous fishes in this study do not appear to be beyond a thermal optimum (i.e. feeding did not decrease at higher temperatures), temperature was an important determinant for feeding rates. Given that many tropical ectotherms are thought to live at or close to their thermal optima (Tewksbury et al., 2008; Sunday et al., 2012), the results of this study suggest that any future change in temperature may have implications for grazing pressure of herbivorous fishes at both the individuals and assemblage level.

While the consistent effect of season on the feeding rates of species with distinctly different diets supports the overall effect of temperature on feeding rates, resource availability (i.e., turf algal cover) influenced feeding rates of two of the eight species examined. Increases in turf algae cover from 45% - 78% resulted in a 79% and 24% increase in the feeding rates of *Zebrasoma velliferum* and *Zebrasoma scopas* respectively. The influence of turf algae availability was relatively weaker than the effect of temperature for the feeding rates of *Zebrasoma scopas*, where feeding only increased by 32% with increases in algal cover versus 87% between winter and summer. In contrast, the influence of turf algae cover was relatively stronger for feeding for *Zebrasoma velliferum*, where feeding increased by 79% with increases to turf algal cover and only 60% between winter and summer. Increases in turf algae availability may provide additional scope for feeding with both reduced search time to locate a resource, and reduced competition which can result in increased feeding, and increased herbivore biomass (Pratchett et al., 2008; Dell et al., 2011; Nash et al., 2016). Furthermore, while not assessed in this study, nutritional quality of algal

turfs may influence feeding, as herbivores are generally nutrient limited (Choat & Clements, 1998; Sterner & Elser, 2002). The nutritional quality and photosynthetic activity of algal turfs are highest in the summer (Klumpp & McKinnon, 1989; Wilson, 2002; Ateweberhan et al., 2006), which could also contribute to the increased feeding rates during the summer seasons.

This study showed that both productivity of turf algae and bite rates of herbivorous fishes vary seasonally, presumably with changing temperature. However, algal productivity was more sensitive to higher temperatures than feeding by herbivorous fishes, leading to a trophic mismatch under increasing temperatures. Such a mismatch may lead to a strengthening of top-down control of algal biomass under warming, which may limit the proliferation of algal turfs into the future. This mismatch may be beneficial for coral reef recovery following disturbance and bleaching events, as increased grazing pressure may create space for new coral recruits (Hughes et al., 2007; Rasher et al., 2013), however it also may lead to dietary resource limitation of consumers.

Chapter 4: Impaired growth and survival of tropical macroalgae (*Sargassum* spp.) at elevated temperatures[3]

4.1 Introduction

Coral reefs are one of the worlds most threatened ecosystems (Walther et al., 2002; Frieler et al., 2013; Hughes et al. 2017), due to the thermal sensitivities of habitat-forming corals, that bleach and die following relatively small increases in temperature (1-2ºC: Baird & Marshall, 2002; Hughes et al. 2017a, b). The increasing frequency and severity of thermal bleaching events has resulted in marked declines in coral cover (Hughes et al. 2017a; 2018a) and shifts in coral composition (Jokiel & Coles, 1990; Berumen & Pratchett 2006; Bento et al. 2016; Hughes et al. 2018b) across many of the world's reefs. These changes, coupled with the collapse of coral recruitment (Hughes et al. 2019) has raised concerns that reefs may not be able to recover, and will become dominated by other benthic taxa, including turf- and macro-algae, that rapidly colonise dead coral skeletons (Diaz-Pulido & McCook, 2002; Hughes et al. 2018b). The potential for these low coral cover reefs to become dominated by algae or other benthic organisms will be dependent on the responses of these benthic organisms to elevated temperatures.

Increasing sea surface temperature (SST) is one of the most pervasive stressors affecting marine ecosystems, driving shifts in species' distribution, phenology, behaviour and community composition (Dell et al., 2011; Vergés et al., 2014; Ling et al., 2015; Hoey et al., 2016; Pinsky et al., 2019). The sensitivities of marine ecosystems to increasing temperature are largely due to the predominance of ectotherms and species (e.g. plants and algae) whose

[3] Graba-Landry, A., Loffler, Z., McClure, E., Pratchett M. S., Hoey, A. S. (2020). Impaired growth and survival of tropical macroalgae at elevated temperatures. *Coral Reefs, 39,* 475-486.

biochemical and cellular processes are largely governed by environmental temperature (Brown et al., 2004). While an organism's upper and lower thermal limits may dictate the range of thermal environments it occupies, within this range the rates of physiological processes (e.g. growth and metabolism) typically increase gradually with temperature until they reach an optimum, beyond which they rapidly decline toward their thermal maximum (Brown et al., 2004; Tewksbury et al., 2008; Bruno et al., 2015). The effect of temperature change on organism performance, therefore, depends on how closely the immediate environmental temperature matches their thermal optimum (Tewksbury et al., 2008; Sunday et al., 2012). Tropical species in particular are thought to have a narrow thermal tolerance range as they have evolved under a relatively invariable thermal environment, and many are thought to live at, or close to their thermal optima (Tewksbury et al., 2008; Sunday et al., 2012).

While there is growing evidence for the negative effects of elevated temperatures on temperate and subtropical macroalgae, the effects of increasing SSTs on fleshy tropical algae has been largely overlooked (Wernberg et al., 2012). Short-term exposure of temperate and subtropical macroalgae to temperatures 3-5°C above ambient has been shown to reduce growth (*Sargassum* spp.; Poore et al., 2013; 2016; Graba-Landry et al., 2018, *Laminaria digitata*; Hargrave et al., 2017), reduce production of chemical defenses (*Laurencia dendroidea*: Sudatti et al., 2011), increase vulnerability to disease (*Delisea pulchra*: Campbell et al., 2011), delay maturation of spores and propagules (*Laminaria* spp.: Lüning, 1988, de Bettignies et al., 2018), but have little to no effect on photophysiology (*Laminaria* spp.; Burdett et al., 2019). However, in some instances there have been positive effects of temperature to algal growth and photosynthesis (*Laminaria ochroleuca*; Hargrave et al., 2017) and primary production (mg O_2 * g dry mass^{-1}, *Canistrocarpus cervicornis*; Hernandez

et al., 2018) under realistic warming scenarios. As such, changes to the properties of the algal thallus (i.e. nitrogen content, physical toughness, growth) as a result of temperature, may come at a cost to other properties within the thallus, as they are often related. For example, thalli which have a high nitrogen content, often have higher rates of growth, which comes at a cost of the physical toughness of the thallus (Sakanishi et al., 2017). Furthermore, any changes to the algal thalli (i.e. nutritional content, physical toughness) as a result of temeprature may also have implications for top-down control of herbivores, who are generally nutrient limited (Mattson, 1980, Huntly, 1990, Clements et al., 2009). Large increases in temperature (>5°C) have led to increased macroalgal mortality, and local extirpation of species from some locations (McCourt, 1984; Wernberg et al., 2013; Smale & Wernberg 2013; Bates et al., 2014) presumably as local environmental temperatures exceed their upper thermal limit. Given the negative effects of temperature on subtropical and temperate algae, it can be predicted that small increases in temperature may have similar or more severe impacts on their tropical counterparts (Koch et al., 2013), which may have implications for macroalgal proliferation following thermally induced coral bleaching events.

Predicting future trajectories of coral reefs under ongoing climate change will not only require an understanding of thermal sensitivities of corals, but also the thermal sensitivities of species that may compete with corals for benthic space. In particular, determining how increasing temperatures affect the growth and survival of tropical macroalgae, and how it varies among life stages, is critical in predicting the likelihood of macroalgal proliferation on coral reefs into the future. The objectives of this study, therefore, were to investigate the effect of elevated temperatures on (i) the growth and survival of recently-settled tropical *Sargassum* propagules, and (ii) the growth and elemental composition of adult tropical *Sargassum*, and (iii) its susceptibility to herbivory.

4.2 Methods

4.2.1 Study Species and Study Site

Sargassum spp. (Phaeophaceae) is a common canopy-forming brown macroalga on coastal reefs worldwide (e.g. Lewis, 1986; Hoey & Bellwood, 2010; Bauman et al., 2017) and often dominates benthic assemblages on degraded coral reefs (Payri & Naim, 1982; Rasher et al., 2013; Chong-Seng et al., 2014). To test the effect of increasing temperature on the growth, survival and palatability of adult and juvenile *Sargassum* spp., a series of experiments were conducted at Lizard Island, northern Great Barrier Reef (14°40'43.842" S, 145°26'52.2924" E). Experiments were conducted from October to November in 2016 and 2017, focussing on *Sargassum swartzii* in 2016, and *Sargassum cristaefolium* and *Sargassum polycystum* in 2017.

Fifty non-reproductive adult thalli (including holdfasts; 10-20 cm in height) of three common and co-occurring species of *Sargassum* (Fucales, Phaeophyta): *S. swartzii* (C. Agardh), *S. cristaefolium* (C. Agardh), and *S. polycystum* (C. Agardh) were collected by hand from reefs in the Turtle Group (14°44'13.11" S, 145°11'48.534" E): a group of inshore reefs in the northern Great Barrier Reef which are located approximately 30 km west of Lizard Island and 15 km from the Queensland coast (Figure 4.1). *S. polycystum* was collected from depths of 0.5-2 m, and *S. swartzii* and *S. cristaefolium* were collected from depths of 1.5-4m within the Turtle Group. Eight *S. swartzii* thalli with mature receptacles were also collected by hand from reefs in the Turtle Group. All thalli were transported to the Lizard Island Research Station in 60 L plastic aquaria and transferred to large 600 L aquaria with fresh flow through seawater and supplemental aeration within 2h of collection. *Sargassum* species were identified using a morphological key (Trono, 1998), and algaebase (Guiry & Guiry, 2020).

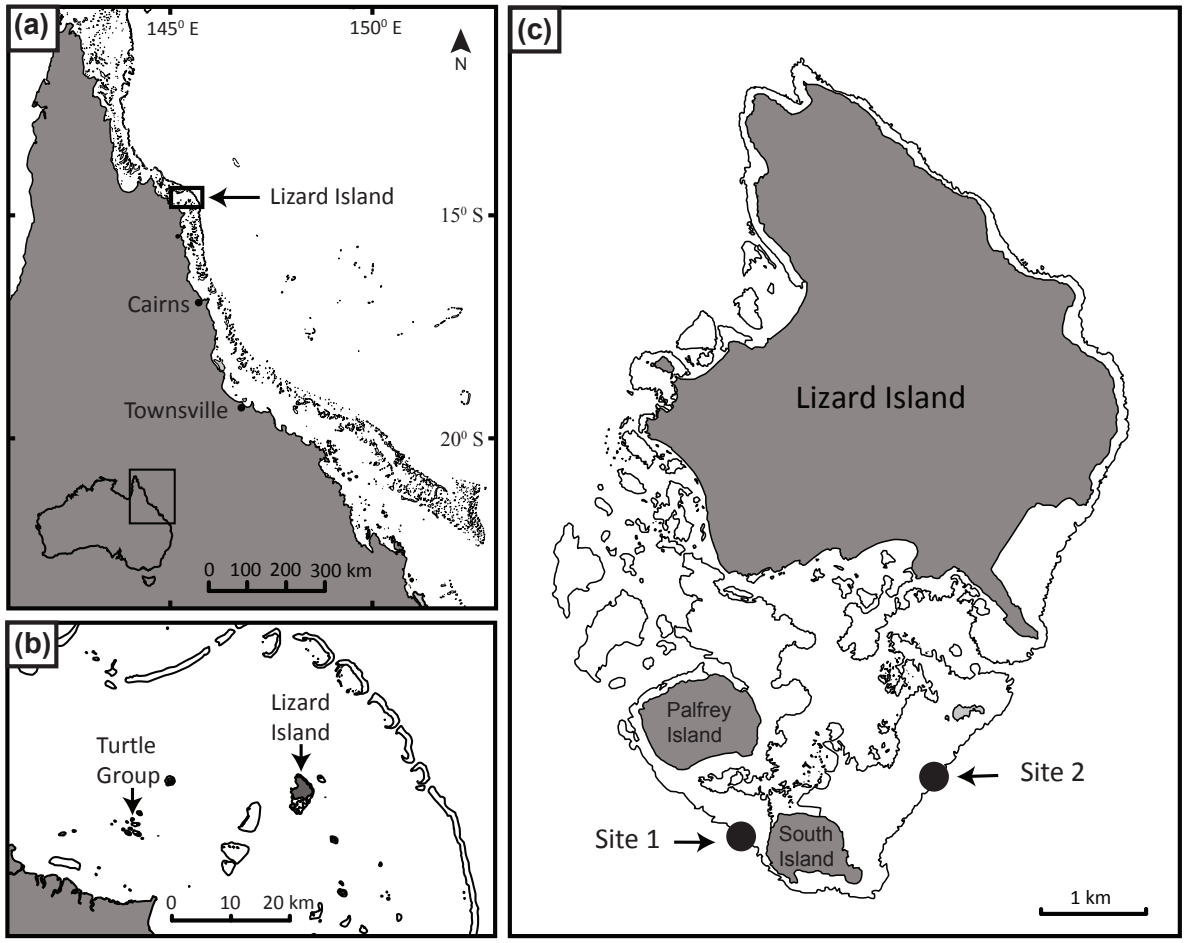

Figure 4.1: Map showing the geographic location of (a) the Lizard Island region in the northern Great Barrier Reef, (b) the Turtle Group and Lizard Island in relation to mainland coast, (c) the two reef crest sites used for the for feeding assays.

4.2.2 Temperature manipulation

Adult thalli and recently-settled propagules of *Sargassum* were exposed to one of three different temperature treatments; ambient (28°C for the propagule experiment, 27°C for the adult thalli experiment), +2°C and +3.5°C. These temperatures were chosen to approximate the minimum (27°C), mean (i.e., 29°C) and maximum (i.e., 30°C-31°C) summer temperatures experienced in the Lizard Island region (AIMS, 2018). While these experimental temperatures are within the range of temperatures experienced by these species at this location, frequency and length of exposure to these temperatures is likely to increase as global SSTs continue to increase (Lough, 2012). Experimental water temperatures were

manipulated in an outdoor experimental system that consisted of three 300 L sumps with 1 KW steel bar heaters and chillers (Teco), with one sump per temperature treatment. Each sump was supplied with fresh seawater at a rate of 515.2 (± 1.73 SE) L hr^{-1} and supplied 10 replicate outdoor 40 L aquaria with the appropriate experimental flow-through seawater using 1000L hr^{-1} pumps (Eheim) at a rate of 51.5 (± 0.11 SE) L hr^{-1}. Individual aquaria and the sumps were wrapped in Insulbreak® insulation to stabilise water temperatures. Light was maintained at levels approximating those at the *Sargassum* collection site in the Turtle Group (9,000 Lux: Hobo Temperature/Light logger). Lux measurements from HOBO loggers were converted to PPFD using conversion factor for sunlight (0.0185: Thimijan & Heins, 1982). Light levels were then replicated (185 μmol photons m^{-2} s^{-1}) in the outdoor laboratory using shade cloth, and monitored (in PPFD) using a handheld quantum sensor (Edaphic Scientific).

4.2.3 The effect of temperature on the growth and survival of Sargassum *propagules*

To determine the effect of water temperature on the growth and survival of early life-stage *Sargassum*, propagules of *S. swartzii* were settled onto terracotta tiles (5cm x 5cm x 1cm) and exposed to one of the three different temperature treatments. One hundred and fifty terracotta tiles (5 cm x 5 cm x 1 cm) were placed at the bottom of a 300 L aquarium with flow-through seawater at ambient temperature (28°C in December) for 24 hours. To stimulate propagule release, the eight reproductively mature *S. swartzii* thalli were removed from their holding aquaria and placed in the sun for approximately 5 hours to desiccate (following Diaz-Pulido & McCook, 2003). After 5h the thalli were transferred to the 300 L aquarium containing the tiles with the water flow turned off, but with supplemental aeration for 48 hours. The thalli were agitated by hand twice daily to further induce propagule release. After 48 hours, the adult *S. swartzii* were removed from the aquarium and a complete water change was conducted by filtering the water in the aquarium through a 20-micron mesh. The tiles with

attached propagules were cultured in the same 300 L aquarium with flow-through seawater for five days before being transferred to the temperature treatments. Individual tiles were randomly allocated to one of the three temperature treatments (i.e., December ambient, +2°C, or +3.5°C) and temperature increased slowly at a rate of approximately 0.5°C per day over a one-week acclimation period, followed by 48-day growth period. Five individual tiles were allocated to one of 10 aquaria (40 L) per temperature treatment (n=49-50 tiles per temperature treatment). Mean experimental water temperatures ± SE for the duration of the experiment were: 28.3°C ± 0.16, 30.2 °C ± 0.05, and 31.9°C ± 0.25 for the 28°C, 30°C, and 31.5°C treatments, respectively..

The density and height of propagules on each tile was quantified at the start of the growth period (day 0), and after a further 5 and 48 days (hereafter day 5 and day 48) by haphazardly placing three replicate 1 cm^2 quadrats onto each tile and counting all propagules within the quadrat using a dissecting microscope. Within each quadrat, the height of three haphazardly chosen propagules were measured using callipers. Mean density (number of propagules per cm^2) and height (mm) were then calculated per tile. Survival was calculated as the proportional change in density from the initial mean per tile (i.e., day 0) and the final mean per tile (i.e., day 5 or day 48). Relative growth rate (RGR (%)) was calculated as percent change in the mean height of propagules per tile.

4.2.4 Effect of temperature on adult Sargassum

To determine the effect of temperature on the growth and susceptibility to herbivores of adult *S. swartzii*, *S. cristaefolium* and *S. polycystum*, individual thalli were exposed to one of three temperature treatments. For each species of *Sargassum*, 45 thalli of similar size (10-20 cm height) with no mature reproductive structures were spun for 30 revolutions in a salad spinner

to remove excess water and weighed (following Hoey, 2010; Bonaldo et al., 2017). Mean initial wet weights ± SE were 19.90 ± 1.08 g, 40.76 ± 2.78 g, 8.95 ± 0.97 g for *S. swartzii*, *S. cristaefolium*, and *S. polycystum*, respectively. Fifteen thalli of each species were haphazardly assigned to each temperature treatment and stocked at a density of three thalli per 40 L aquaria. Individual thalli were tagged using a small plastic label attached to the holdfast. Within each aquarium, thalli were separated by at least 10 cm. The position of each thallus within the tank was constant throughout the experiment. Temperature in the experimental aquaria was slowly increased at a rate of approximately 0.5°C per day over a one-week acclimation period, followed by a 2-week growth period. Temperature (± 0.2°C) was measured at least three times daily using a portable temperature probe (Comark) calibrated to 26°C, 28°C and 30°C (National Association of Testing Authorities Certified). Mean temperatures (± SE) for the duration of the 2016 experiment were 27.2°C ± 0.03, 28.9 °C ± 0.03, and 30.4 °C ± 0.03 for the ambient (27°C), +2°C (29°C), and +3.5°C (30.5°C) treatments, respectively. In 2017, experimental temperatures were 26.5°C ± 0.02, 29.4°C ± 0.10, and 30.4°C ± 0.04 for the ambient (27°C), +2°C (29°C), and +3.5°C (30.5°C) treatments, respectively. Following the 2-week growth period, individual thalli were spun and weighed as described above. Relative growth rate was calculated as the percent change in wet weight (%) between the initial and final mass of each thallus.

The physical toughness of three randomly selected blades from each thallus (n=45 per species, per temperature treatment) was measured for each of *S. swartzii*, *S. cristaefolium* and *S. polycystum* using a penetrometer (following Duffy & Hay, 1991). Briefly, a *Sargassum* blade was secured between two flat aluminium plates with a 5mm hole in the centre of the plates. A flat-headed pin (5 mm diameter) was then placed in the hole, with a small vessel secured at the top of the pin. Mass was incrementally added to the vessel until the pin pierced

completely through the algal tissue. The weight (including the vessel and pin) was measured using a balance (0.01g) and used as proxy of the physical toughness of the blades (Duffy and Hay 1991).

To quantify any changes in the carbon and nitrogen (% dry weight (DW)) composition of *Sargassum* five thalli of each species from each temperature treatment were haphazardly selected. From each of the selected thalli, a small sample (~ 0.2 g wet weight) from the upper portion of a branch which contained a blade, stipe and meristematic tissue (see Graba-Landry et al., 2018), was rinsed with fresh water, and freeze dried. Samples were sent to OEA Laboratories (Plymouth, UK) for homogenization and elemental analysis using a radio mass spectrophotometer.

4.2.5 Susceptibility of Sargassum *to herbivores*

To determine whether temperature influenced the susceptibility of adult *S. swartzii, S. cristaefolium* and *S. polycystum* to herbivores, a series of cafeteria-style feeding assays were conducted. For each species of *Sargassum*, three thalli (one from each temperature treatment) were haphazardly selected, spun and weighed (as previously described) and woven between the strands of short lengths (1 m) of 3-ply rope (following Bonaldo et al., 2017; Rasher et al., 2017). The order in which thalli were woven into ropes was randomised among replicates. These experimental ropes were secured along the substratum at two reef crest sites at Lizard Island (Figure 4.1c). For each species of *Sargassum*, two ropes were deployed each day at each site; one exposed to the local herbivore assemblage, and one placed inside an exclusion cage (9,000 cm^3, 1 cm^2 galvanized wire mesh) to control for the effects of handling and translocation. A small stationary video camera (GoPro Hero 2 or 3) mounted on a dive weight was positioned approximately 1 m from the thalli exposed to local herbivore

assemblages to record any feeding activity on the *Sargassum* thalli. A 30 cm ruler was held adjacent to the *Sargassum* thalli for ~10s at the start of each video to provide a scale. After 3h all thalli were retrieved, spun and weighed (as above). The reduction in *Sargassum* biomass due to herbivory was estimated as: $[T_i \times (C_f/C_i)] - T_f$, where T_f and T_i are the final and initial mass of the thalli exposed to herbivores and C_f and C_i are the final and initial mass of the control thalli (Cronin & Hay, 1996).

The video footage was analysed and the fish species, total length, and number of bites taken on each of the *Sargassum* thalli was recorded. To account for body-size related differences in the impacts of individual bites, mass-standardized bites were calculated as the product of the body mass of each fish and the number of bites it was observed to have taken (following Bellwood et al., 2006). The mass of individual fish were determined using published length-weight relationships for each species (Hoey et al., 2013; Froese & Pauly, 2018). Video trials were terminated when only the stipe remained of one the thalli and there was no choice available.

4.2.6 Statistical Analysis

Data on growth and physical toughness of adult thalli were analysed using linear mixed effects models following a gaussian distribution with ‘Temperature’ as a fixed factor and ‘Tank’ as random blocking factor using the ‘nlme’ package in R (Pinheiro et al., 2018). Model selection was determined by comparing Akaike Information Criterion values for small sample sizes (AICc) using the “MuMIn” package (Bartón, 2018). For the analysis of physical toughness, individual thallus (‘Individual’) was also included as a random blocking factor as three blades were sampled per thallus. The carbon and nitrogen content of all three species was analysed using linear models fit with a gaussian distribution, with ‘Temperature’ as a

fixed factor. 'Tank' was not included in the model as each sub-sample was taken from a different tank. Data on the reduction in *Sargassum* biomass and the mass standardized bites recorded on the assays were analysed using linear mixed effects models with temperature as a fixed factor and experimental rope ('Rope') as a random factor to account for non-independence using the 'lme4' package (Bates et al., 2015). As survival data for the propagules was calculated as a proportion, a binomial distribution with a logit link function was used in the linear mixed effects model with 'Temperature' and 'Time' as fixed factors and 'Tank' as a random factor using the "lme4" package. Growth of propagules was analysed using a linear mixed effects model with a gaussian distribution with 'Temperature' and 'Time' as fixed factors and 'Tank' as a random factor using the 'nlme' package. Maximum likelihood was used to compare between models with fixed effects only and restricted maximum likelihood was used when comparing mixed effects models. When significant differences among treatments were detected, *post hoc* Tukey pairwise tests were conducted with the 'glht' function ("Multcomp" package). All model residuals were tested for normality and homogeneity of variance using diagnostic plots (ie: Q-Q plots and residual vs. fitted plot respectively). When necessary, data were transformed to meet assumptions.

4.3 Results

4.3.1 The effect of temperature on the growth and survival of Sargassum propagules

Temperature was included in the best fit models for both survival and growth of *S. swartzii* propagules (Table C1). The survivorship of *S. swartzii* propagules displayed a similar trend across all temperature treatments, with an initial rapid decline (0.34 – 0.51 surviving after 5 days) followed by a period of increased survivorship (0.02 – 0.11 of propagules surviving until day 48). There were however, differences in survival among temperatures. The survival

of propagules cultured at +3.5°C was 12-33% and 78-84% less than propagules cultured at ambient (28°C) and +2°C at 5 and 48 days respectively (Figure 4.2a, Table C2).

The relative growth rate of *S. swartzii* propagules was influenced by temperature, with the highest growth rates recorded in the lowest temperature (ambient: 28°C), and the lowest growth rates at the highest temperature (+3.5°C) after 5 and 48 days of exposure (Figure 4.2b, Tables C1, C2). After 48 days the relative growth rate of *S. swartzii* propagules cultured at 30.5°C (161.55% ± 20.71 SE) was 43% lower than propagules cultured at ambient temperature (285.60% ± 23.02 SE; Figure 4.2b, Tables C1, C2).

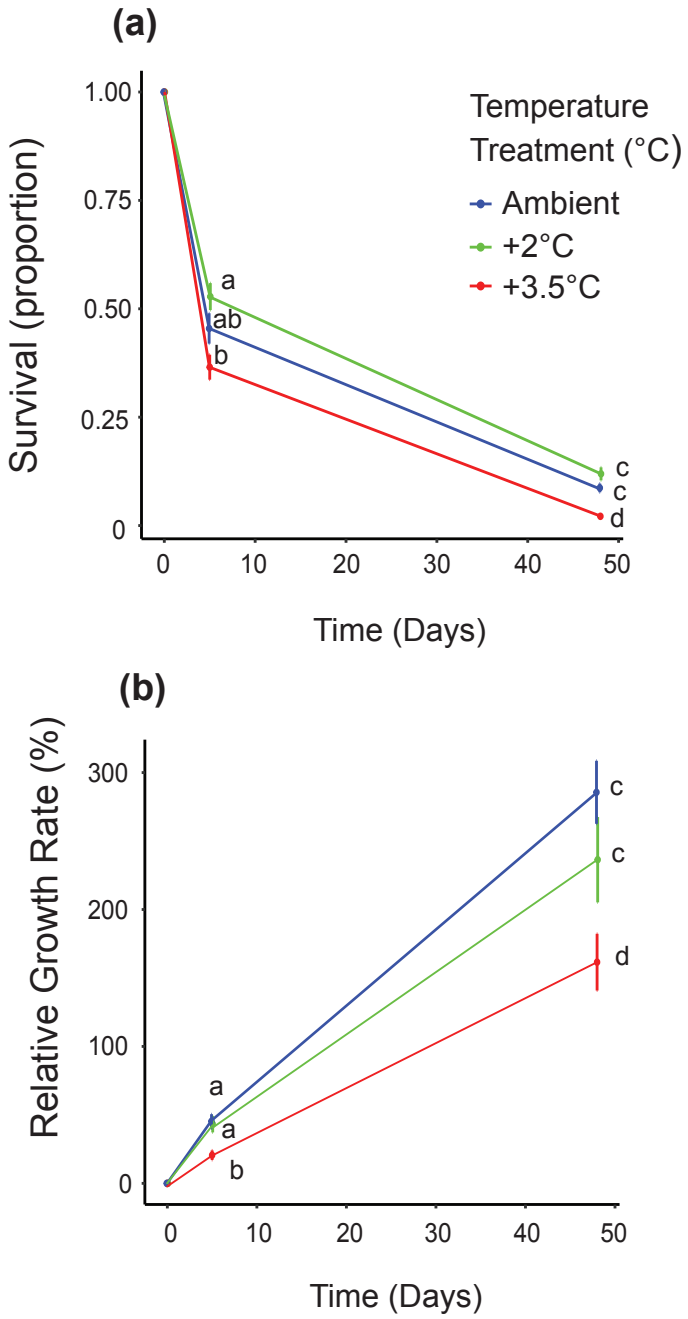

Figure 4.2: The effect of temperature on the survival (a) and relative growth rate (b) of *Sargassum swartzii* propagules reared in three temperature treatments after 5 and 48 days. Data are means ± SE, n=49-50.

4.3.2 The effect of increased temperature on adult Sargassum

Temperature was included in the best fit models for the growth of adult thalli of all three *Sargassum* species, physical toughness (for *S. cristaefolium* only), nitrogen content (of *S. polycystum*, and *S. crisaefolium*), and mass removed by herbivores (*S. swartzii* and *S. cristaefolium*) (Table C3).

The growth of all three *Sargassum* species was adversely affected by increasing temperature with the lowest growth rates for all three species being recorded at the highest (+3.5°C) temperature (Figure 4.3a, Table C4). *S. swartzii* and *S. cristaefolium* displayed negligible change in biomass when held at ambient (27°C) and +2°C for 2-weeks, but a significant decline in biomass of -17.55% ± 4.17 SE and -16.92 % ± 3.17 SE, respectively at +3.5°C (Figure 4.3a, Table C4). In contrast, the biomass of *S. polycystum* increased under all temperature treatments, with the greatest increase at ambient temperature (27°C) (55.10% ± 9.68 SE) compared to 30.64% ± 5.70 SE and 27.98% ± 6.47 SE in the +2°C and +3.5°C treatments, respectively (Figure 4.3a, Table C4).

Temperature was found to influence the physical toughness of one of the three *Sargassum* species examined with the mass required to pierce the blades of *S. cristaefolium* decreasing by approximately 18% for thalli cultured at +3.5°C compared to thalli cultured at ambient and +2°C (Figure 4.3b, Table C4). The mass required to pierce the blades of *S. polycystum* (range: 678.36 g ± 44.68 SE at +3.5°C to 699.88 g ± 57.37 SE at ambient temperature) and *S. swartzii* (range: 732.80 g ± 49.01 SE at ambient to 781.27 g ± 39.21 SE at +2°C) did not differ between temperatures (Figure 4.3b, Table C4).

Temperature had significant and opposing effects on the nitrogen content of *S. cristaefolium* and *S. polycystum* where mean nitrogen content increased in *S. cristaefolium* (from 0.48% ± 0.04 SE to 0.56% ± 0.01 SE) between the ambient and +3.5°C temperature treatments and decreased in *S. polycystum* (from 0.73% ± 0.02 SE to 0.58% ± 0.04 SE) between the +2°C to the +3.5°C temperature treatments (Figure 4.3c, Table C3, C4). Temperature had no effect on carbon content, or the carbon:nitrogen ratio of all 3 species (Figure C1, Table C3).

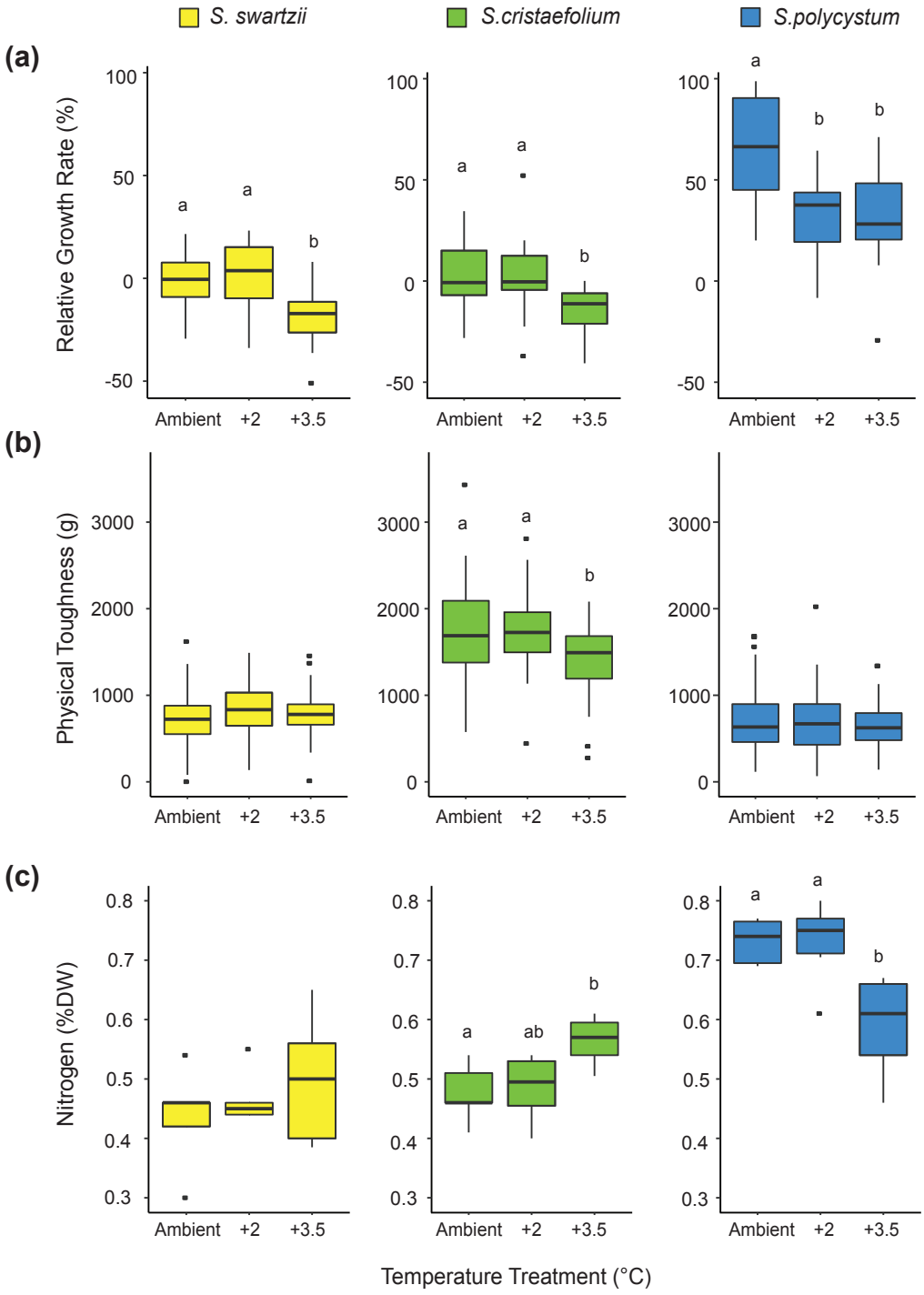

Figure 4.3: The effect of temperature on the (a) relative growth rate (n=13-15), (b) physical toughness (n=45), and (c) nitrogen content (n=5) of *Sargassum swartzii*, *Sargassum cristaefolium*, and *Sargassum polycystum*. Boxplots show the median and inner quartiles. Physical toughness is the mass required to force a 5mm blunt pin through an individual blade. Letters indicate homogenous subsets identified in *post hoc* Tukey's tests.

4.3.3 Susceptibility of Sargassum *to herbivores*

When exposed to local herbivore assemblages on the reef crest the reduction in algal biomass was greatest for *S. swartzii* and *S. cristaefolium* cultured at ambient water temperature (i.e., 27°C) and decreased with increasing temperature (Figure 4.4a; Tables C3, C4). For both *S. swartzii* and *S. cristaefolium* the reduction in algal biomass was approximately 2-fold greater for thalli cultured at ambient (*S. swartzii*: 12.02 g ± 2.37 SE; *S. cristaefolium*: 7.66 ± 2.65 SE) than thalli cultured at +3.5°C (*S. swartzii*: 6.02 ± 1.11 SE; *S. cristaefolium*: 2.60 g ± 1.40 SE; Figure 4.4a). There were no differences in mass removed from *S. polycystum* across temperature treatments (Figure 4.4a, Table C3).

Two fish species, the blue spine unicornfish (*Naso unicornis*) and the two-barred rabbitfish (*Siganus doliatus*) accounted for 83% of all bites recorded across the three *Sargassum* species. Feeding by "other" species (i.e., *Siganus corallinus*, *Acanthurus blochii*, *Acanthurus dussumieri*, *Acanthurus nigrofuscus*, and *Ctenochaetus striatus*) accounted for the remaining 17% of bites, however feeding by these species was highly variable and precluded formal analysis (Table C6). There were no detectable differences in feeding by the entire herbivore assemblage, or *N. unicornis* and *S. doliatus* independently from thalli cultured at different temperatures (Figure 4.4b, Table C4, Table C5).

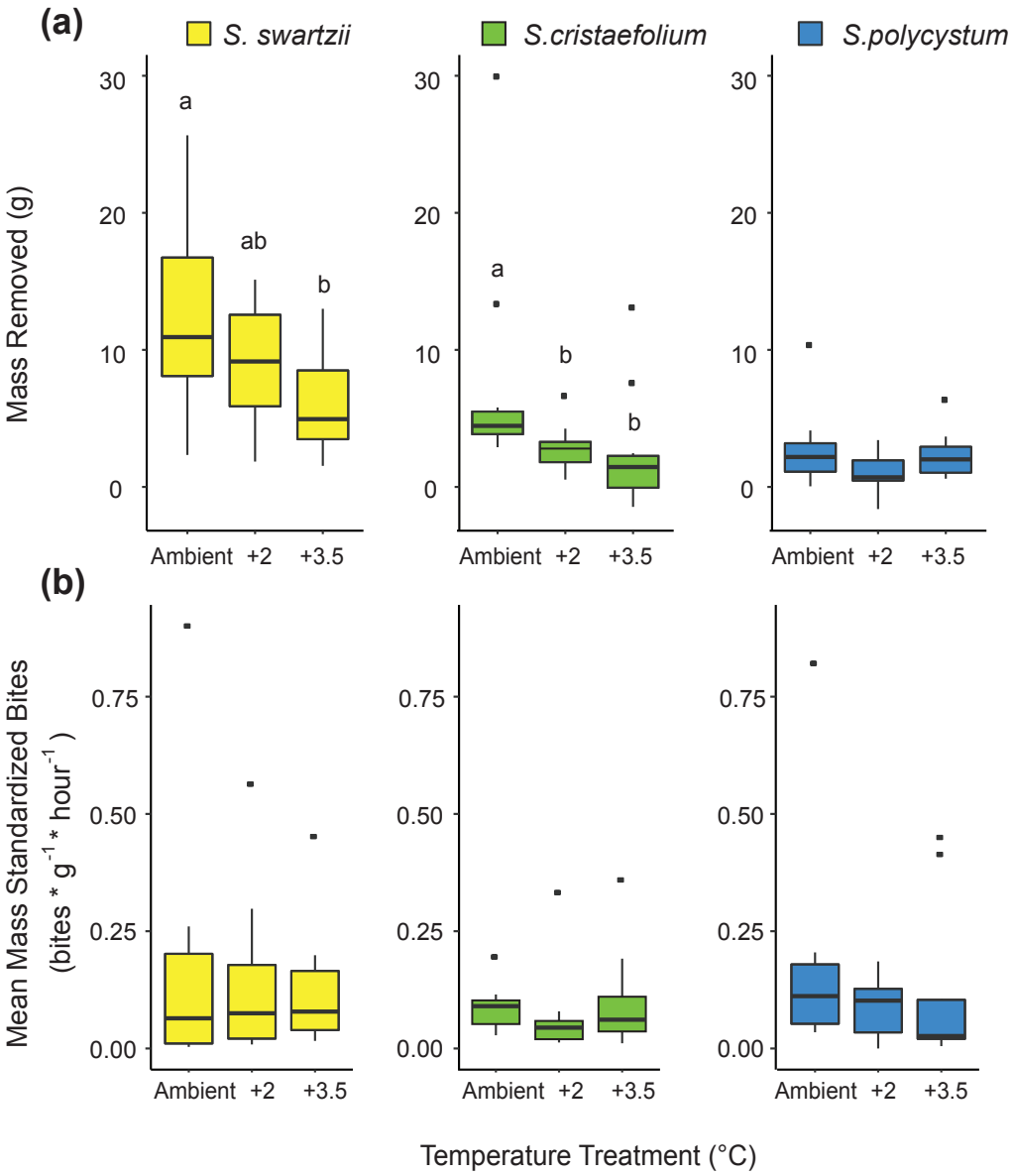

Figure 4.4: The effect of temperature on the susceptibility of *Sargassum* to local herbivore assemblages on Lizard Island, (a) reduction in *Sargassum* biomass of thalli from different temperature treatments exposed to local herbivore assemblages and (b) mean mass standardized bites (bites * mass of fish $(g)^{-1}$ * $hour^{-1}$) by different herbivorous fish species on thalli from different temperature treatments. Data that do not share a letter differ in *post-hoc* Tukey's tests. n=10. Boxplots show the median and inner quartiles.

4.4 Discussion

Extensive and widespread coral loss as a result of increasing temperature is reinforcing long-held concerns that coral will be replaced by fleshy macroalgae and other benthic organisms as the dominant biota on coral reefs (Bellwood et al., 2004; Hughes et al., 2007; Graham et al., 2015). Our results demonstrate that like corals, tropical *Sargassum* spp. are adversely affected by predicted (+2-3.5°C) increases in temperature. The survival and growth of *S. swartzii* propagules was 88% and 38% lower at +3.5°C compared to +2°C, respectively. Similarly, the growth of three species of adult *Sargassum* was reduced by ca. 45% after short term (2-week) exposure to elevated temperatures. Importantly, local populations of *Sargassum* within this region of the GBR are already experiencing temperatures equivalent to our experimental temperatures (AIMS, 2018), but only for relatively short periods. Given ongoing climate change, exposure to these current day 'extreme' temperatures are predicted to become more frequent and more severe (Lough, 2012), limiting the potential for the establishment of new, and the persistence of existing *Sargassum* populations in a warming ocean.

The early post-settlement period is widely viewed as a critical period for marine organisms, with rates of early post-settlement survival often disrupting patterns established at settlement, and directly influencing adult populations (Forrester, 1995; Kendrick & Walker, 1995). Survival of newly settled *Sargassum* propagules *in situ* is extremely low (0.0001%; 2-3 months post-settlement; Kendrick & Walker, 1995) and as such any changes to the number of individuals surviving this early life history stage will directly affect local populations. A 3.5°C increase in temperature led to an 84% decline in the survival of *Sargassum* propagules over 48 days in the present study relative to propagules cultured at ambient (i.e., 28°C) and +2°C temperature treatments. Moreover, propagules cultured at 3.5°C above ambient were

50% smaller than those cultured at ambient (28°C) temperature after 48 days. This reduced growth and hence smaller size will likely render propagules more susceptible to incidental grazing than faster growing and larger propagules (Diaz-Pulido & McCook, 2003), and will delay the time until they reach a size refuge from grazing herbivores (Hoey & Bellwood, 2009). Such mortality and reduced growth of *Sargassum* propagules is not only likely to constrain the replenishment of existing populations, but also the establishment of *Sargassum* in new areas (Kendrick & Walker, 1995). Reduced recruitment of habitat-forming macroalgae (e.g., *Ecklonia radiata, Scytothalia dorycarpa*) following acute temperature increases have been documented in subtropical marine ecosystems (Wernberg et al., 2013; Andrews et al., 2014). Furthermore, short term (2-8 weeks) exposure to experimental increases in temperature (+2-4°C above the summer mean) have resulted in a ~25% reduction in growth and a 25-50% reduction in survival of propagules of temperate and subtropical fucalean macroalgae (Chu et al., 2012; Alestra & Schiel, 2015). The magnitude of these responses of temperate and subtropical macroalgae were, however, smaller than the tropical *S. swartzii* in our study which exhibited a 43% reduction in growth and a 85% reduction in survival. Tropical macroalgae (such as *Sargassum*) may therefore, be more vulnerable to small increases in temperature than their subtropical counterparts.

Together with the reduced growth and survival of *Sargassum* propagules, reductions in the growth of adult *Sargassum* thalli at elevated temperatures are likely to restrict the accumulation of *Sargassum* biomass and may cause earlier onset of senescence under ongoing ocean warming. While the variation in relative growth rates among *Sargassum* species may reflect their habitat, with *S. polycystum* generally occurring in shallow (0.5-2 m), and likely thermally variable habitats (Harborne, 2013) and *S. swartzii* and *S. cristaefolium* in deeper (1.5-4 m), and likely thermally stable, habitats at our collection sites (A. Hoey pers.

obs), the similar declines in growth rate suggest that the current summer maximum temperature (30.5°C) may exceed their thermal optima for growth. Comparable declines in photosynthesis (*Codium edule*: Lee & Hsu, 2009) and net productivity (*Sargassum fluitans, Dictyota menstrualis, Laurencia chondroides*; Anderson, 2006) have also been documented in a range of tropical macroalgae after short-term exposure to temperatures 1-3°C above local summer mean. Further, two of the three species examined in the present study (*S. swartzii* and *S. cristaefolium*) exhibited negative growth when cultured at current summer maximum temperatures (30.5°C) for 2 weeks. This senescence is likely due to the direct effect of temperature rather than interspecific variation to phenology as experimental thalli lacked reproductive structures. The consistency of the declines in growth, photosynthesis, and productivity indicate that many tropical macroalgal taxa may be occupying areas close to their thermal optima.

While previous studies have suggested the susceptibility of macroalgae (such as *Sargassum*) to herbivores may be related to nutritional content or physical toughness (Steinberg & Paul, 1990; Clements et al., 2009) this study found no evidence to support this. For example, the increased nitrogen content and decreased physical toughness of *S. cristaefolium* at elevated (+3.5°C) temperatures should make the thalli more palatable to herbivores, however this was not reflected in the field feeding assays. Therefore it may be possible that the thalli cultured at elevated temperatures are senescing and less palatable to the same suite of herbivores (Lefévre & Bellwood, 2011). Increased microbial activity, altered microbial communities, or binding activities of the detrital cell wall associated with the senescence of *Sargassum* thalli may increase the nitrogen content (Hanisak, 1993; Campbell et al., 2011; Webster et al., 2011), and reduce physical toughness of the thallus. The preference for *Sargassum* thalli cultured at lower temperatures could indicate that under

future elevated temperatures the macroalgal biomass removed by browsing herbivores may be reduced, however this will also be dependent on the response of herbivorous fishes to elevated temperatures. While the reduced consumption of *Sargassum* cultured at elevated temperatures could be argued to compensate for the reduced growth of these thalli, it should be noted that local herbivorous fish assemblages were presented with a choice of *Sargassum* cultured under different temperatures. The potential accumulation of *Sargassum* biomass under future warmer conditions will not only depend on rates of growth and consumption, but also the availability of other potential food sources for browsing fishes (Choat & Clements, 1998; Clements et al., 2009). Any reductions in growth and consumption of macroalgae could also restrict the flow of macroalgal based production entering the food web. Altered energy flow from the producer level may have flow-on effects to higher trophic levels (Hawlena & Schmitz, 2010), and nutrient cycling throughout the ecosystem (Hanisak, 1993; O'Neil & Capone, 2008; Pessarrodona et al., 2018).

The strong negative effects on growth and survival of *Sargassum* to increasing temperature observed in this study may be due to the short term nature of the exposure to elevated temperatures. Such short-term exposures to elevated temperatures are increasingly relevant given both realised and predicted increases in acute marine heatwave events (Hughes et al. 2017a; 2018b; Oliver et al. 2018). Indeed, marked reductions in canopy-forming macroalgal biomass have already been recorded following marine heatwaves (1-2°C above maximum summer temperatures for 8-10 weeks) in both temperate and subtropical regions (McCourt, 1984; Wernberg et al., 2013). But there may also be potential for macroalgae to adapt to long term warming. Sessile organisms must rely on physiological mechanisms driven by changes to gene expression: phenotypic plasticity or adaptation (King et al., 2019). Such changes can lead to differences in thermal tolerances (i.e. adaptive capacity e.g.

Undaria pinnatifida and *Egregia menziesii*; Henkel & Hofmann, 2008), or to different morphologies (phenotypic plasticity e.g. *Hormosira banksia*; Clark et al., 2018) among different populations across latitude. Therefore the results of this study, which only investigated the effect of temperature to one population for each species, may not be representative of the entire distribution of the species. Further research is required to examine the effects of temperature on *Sargassum* at both the centre and edges of the thermal range to determine between-population variability in thermal tolerance.

Although macroalgae are widely viewed as potential 'winners' of increasing temperatures on coral reefs, our findings question this view. Clearly, increasing ocean temperatures are challenging for tropical species, more so than for their subtropical and temperate counterparts (Kordas et al., 2011; Sunday et al., 2012; Koch et al., 2013). Short-term exposure to elevated temperatures that are already being experienced on local reefs have led to deleterious effects to at least three species of tropical *Sargassum*. Predicted increases in temperature due to ongoing climate change may, therefore, not only lead to a loss of live coral, but also loss of other major habitat-forming macroalgae, leading to novel reef ecosystems that are both low in coral and macroalgae cover.

Chapter 5: Temperature-driven metabolic mismatch in a coral reef fish: key species unlikely to meet metabolic demands in a warming ocean[4]

5.1 Introduction

Increasing sea surface temperature (SST) is the foremost effect of climate change on marine ecosystems worldwide (Walther et al., 2002; Bindoff et al.., 2019). The susceptibility of marine ecosystems to increasing temperatures are underpinned by the thermal sensitivities of individual species, with ectotherms being particularly vulnerable as their rates of biochemical and physiological processes are governed by environmental temperature (Brown et al., 2004). Within a species' thermal tolerance range, the relationship between the rates of physiological processes and temperature is generally a left skewed curve such that the temperature at which performance peaks (i.e., a thermal optimum) is closer to their upper than their lower thermal limit (Huey & Stevenson, 1979). The physiological response of an individual to increasing temperature will therefore depend on how closely an organism is living in relation to its thermal optimum, and the breadth of its thermal tolerance range (Tewksbury et al., 2008; Sunday et al., 2012). Tropical marine ectotherms are thought to be the most vulnerable group to increasing temperatures as they have evolved under relatively stable thermal conditions and have a narrow thermal tolerance range, with most species living at, or close to, their thermal optimum with limited thermal refugia available (Tewksbury et al., 2008; Sunday et al., 2012; Pinsky et al., 2019).

The capacity of an individual to meet increasing metabolic demands under elevated temperatures will depend on the availability and uptake of sufficient energy (Huey &

[4] Graba-Landry, A., Laubenstein, T., Pratchett M. S., Hoey, A. S. Temperature-driven metabolic mismatch in a coral reef fish: key species unlikely to meet metabolic demands in a warming ocean. *(In prep)*

Kingsolver, 2019). In salmon, for example, increasing temperature has been shown to result in smaller, less heat tolerant individuals when food is limited, likely due to the increased energetic costs of increased metabolism (Brett, 1971; Huey & Kingsolver, 2019), but when food is not limiting, individuals are able to increase consumption rates to compensate for increased metabolic demand (Koskela et al., 1997). However, there is often a mismatch in the rates of change of metabolism and consumption with increasing temperature, where increasing temperature has been shown to have a greater effect on metabolic rates than consumption rates across a wide variety of temperate and arctic marine, terrestrial and freshwater taxa (Brett, 1971; Vucic-Pestic et al., 2010; Rall et al., 2011; Lemoine & Burkepile, 2012; Alcaraz et al., 2014; Iles, 2014; Mertens et al., 2015), leading to energy deficits and reductions in consumer fitness at elevated temperatures (Lemoine & Burkepile, 2012). Predicting consumer fitness under future warming requires an understanding of the relationship between consumption (energy acquired) versus metabolism (energy required) of consumers as temperatures increase (Rall et al., 2010; Iles, 2014). To date, the majority of studies investigating the effect of temperature on tropical marine ectotherms have focussed one or two physiological metrics in isolation, commonly aerobic metabolism and growth in coral reef fishes (e.g. Nilsson et al., 2009; Gardiner et al., 2010; Rummer et al., 2014) and have not considered the broader effects of increasing temperature on individual fitness and feeding behaviour.

On coral reefs, herbivorous fishes are widely-viewed as important functional species responsible for maintaining algal communities in a cropped state, and creating space for corals to settle and grow (McCook et al., 2001; Cheal et al., 2010; Hughes et al., 2007; 2010), yet relatively little is known of how they will respond to increasing temperatures. I used the common barred rabbitfish (*Siganus doliatus*) to test the effect of temperature on

rates of metabolism, feeding, growth and energetic reserves. Specifically I asked: (1) Do feeding and metabolic rates scale similarly as temperature increases? (2) Are there any physiological cost associated with a potential mismatch between feeding and metabolic rates?

5.2 Methods

5.2.1 Study Species and Specimen Collection

Siganus doliatus is an ecologically important species as it is one of the few nominally 'herbivorous' fish species on the Great Barrier Reef (GBR) that will target fleshy brown macroalgae (Fox & Bellwood, 2007; Mantyka & Bellwood, 2007; Fox & Bellwood, 2008; Bennett & Bellwood, 2011; Hoey et al., 2013), and has a widespread distribution across the GBR (Cheal et al., 2012). Thirty juvenile *Siganus doliatus* (mean wet weight: 28.68 g ± 2.54 SE) were collected using hand and barrier nets from Orpheus Island (18.6161°S, 146.4972°E) and Pelorus Island (18.5541°S, 146.4869°E), inshore reefs of the central Great Barrier Reef (GBR), Australia. Individuals were transported to Orpheus Island Research Station (OIRS) within one hour of collection in 60 L aquaria fitted with portable aerators and placed in a 300 L holding tank for a maximum of three days. Individuals were then placed in 25 L drums with fresh seawater (maximum density of 10 individuals per drum) fitted with portable aerators and transported to the Marine and Aquaculture Research Facility Unit (MARFU) at James Cook University, Townsville. Each individual *S. doliatus* was transferred to separate 72 L aquaria with a PVC shelter and supplemental aeration, and were left to acclimate to the experimental setup at ambient temperature (~28°C) and salinity (35 ppt) for a minimum of 3 weeks prior to experimentation. Individuals were fed *ad libitum* on commercial fish feed pellets (Primo G12, Ridley Aquaculture), and green macroalgae *Ulva* sp. twice daily during the acclimation period and for the duration of the experiment.

5.2.2 Temperature Manipulation and Experimental Set-Up

Seven or eight juvenile *S. doliatus* were exposed to one of four different temperature treatments; 26°C, 28°C, 30°C and 32°C for 8 weeks in total. Individual fish were haphazardly allocated to one of the four temperature treatments and there were no differences in initial sizes of individual fish between treatments (Table D1). These temperatures were chosen to approximate the summer minimum (i.e., 26°C), summer mean (28°C), summer maximum (30°C) and +2°C above summer maximum (32°C) temperatures experienced in the Orpheus Island region (AIMS, 2020). While tropical coral reefs are warming at 70% the global average, the frequency and length of exposure to summer maximum temperatures are likely to increase due to global warming (Lough, 2012).

Experimental temperatures were manipulated in four sumps with individual 3KW steel bar heaters and chillers, with one sump per temperature treatment. The target temperature in each sump was maintained by a digital thermostat (TIC-17RGT, Full Gauge), which was calibrated weekly, and temperature was recorded hourly. Each sump delivered treatment water to replicate 72 L aquaria (n= 7 for 28°C and 32°C/ n=8 for 26°C and 30°C treatments). For full detail of experimental set up and recirculating seawater filtration, refer to Appendix D. From the acclimation temperature (28°C), experimental temperature was slowly increased/decreased at a rate of ± 0.3°C per day until the treatment temperatures were met. Treatment temperatures (± SE) were: 25.96°C (± 0.01), 28.39°C (± 0.01), 29.95°C (± 0.01), 31.93°C (± 0.01) for the 26°C, 28°C, 30°C, and 32°C temperature treatments, respectively. Feeding assays were conducted after fish had been held in the treatment temperature (after ramp-up) for 3.5 weeks, respirometry trials were conducted after 4 weeks, and growth and body condition index were measured after 6 weeks (i.e., once all of the respirometry trials were completed). Respirometry trials were conducted over 10 days.

5.2.3 Respirometry: Resting Oxygen Uptake

Oxygen uptake is commonly used as a proxy for metabolic rate, and oxygen uptake when an organism in the exclusion of activity is used as a proxy for resting metabolic rate, and is commonly used to predict the responses of metabolism to temperature (Killen et al., 2007; Clark et al., 2013). To estimate the effect of rearing temperature on metabolic rate of juvenile *S. doliatus* I quantified the resting oxygen uptake ($MO_{2\ rest}$) of individual fish using intermittent flow respirometry, following 'best' practice (Clark et al., 2013; Svendsen et al., 2016). Briefly, fish were starved 24 hours prior to experimentation to ensure digestive metabolism did not interfere with resting oxygen uptake (Niimi & Beamish, 1974). Individual fish were then placed into 1.7 L (1.972 L including tubing) darkened glass respirometry chambers fitted with a bevel to restrict fish movement. The respirometry chambers where submerged in a 270 L aquaria supplied with UV filtered seawater from the individual's treatment temperature treatment. Small (200 L/hr) submersible pumps (AquaPro) fitted to each chamber supplied a continuous flow from the surrounding water bath. The submersible pumps were controlled using the purpose built python program: AquaResp (v.3, University of Copenhagen, aquaresp.com) to intermittently open and close the fish chamber to flush/wait/measurement periods (following Svendsen et al., 2016). Each chamber was fitted with a temperature-calibrated oxygen dip probe (OXROB3 Robust Oxygen Probe, PyroScience, Achen, Germany) fitted and sealed within its own receptacle. Flush/wait/measurement periods varied with the size of fish and water temperature to ensure oxygen saturation did not go below 80% for the duration of the trial (Range: 360 – 600 seconds/60-210 seconds/270-390 seconds for Flush/Wait/Measurement periods). Fish remained in respirometry chambers for 24 hours. Oxygen consumption within the chamber was determined by a linear regression of the oxygen level during the measurement (closed) period. Background microbial respiration, measured before and after each trial, was

subtracted from the total chamber respiration (assuming linearity) to accurately calculate the $MO_{2\ rest}$ of the fish (following Rummer et al., 2014). The value of MO_{2rest} for each fish was calculated as the average of the lowest 10% of MO_2 values which had an $R^2 > 0.9$ (following (Roche et al., 2013; Rummer et al., 2014; Laubenstein et al., 2019).

5.2.4 Feeding Assay

To determine the effect of increasing temperature on feeding rate and feeding selectivity a cafeteria-style feeding assay was conducted using the macroalgae *Sargassum*, *Padina*, and *Lobophora.* Fifty thalli of each of type of macroalgae (*Sargassum* sp., *Padina* sp., and *Lobophora* sp.) were collected by hand from Magnetic Island, Queensland, Australia (19.1547°S, 146.8452°E), and transported in 60 L plastic aquaria fitted with portable aerators to MARFU within 1 hour of collection. *Sargassum*, *Padina*, and *Lobophora* are common macroalgae on inshore reefs of the GBR (Johns et al., 2018), are consumed by adult *S. doliatus* (Hoey et al., 2013), have varying nutritional profiles (Angell et al., 2012), thalli toughness (Steinberg & Paul, 1990), and palatability to herbivorous fishes (Mantyka & Bellwood, 2007; Loffler et al., 2015).

Fish were starved for 24 hours prior to experimentation to ensure that prior feeding did not interfere with the trial. One individual thallus of similar size (~3 cm height) of each of the three macroalgae species (*Sargassum*, *Padina*, and *Lobophora*) was haphazardly selected, spun in a salad spinner and weighed and woven between the strands of short lengths (20 cm) of 3-ply rope (following Bonaldo et al., 2017; Rasher et al., 2017). The order in which thalli were woven into ropes was randomised among replicates. The experimental ropes were secured along the bottom of each individual aquarium and a small stationary cameras (Go Pro) positioned above the aquarium recorded feeding activity continuously for three hours.

The video footage was analysed blind (i.e. the viewer did not know the temperature treatment) and the number of bites taken on each of the macroalgal species, as well as the biofilm on the base and walls of the aquaria was recorded. Video trials were terminated if a thallus was entirely consumed, therefore removing the choice. The sum of all bites across all thalli were calculated to estimate an overall feeding rate.

5.2.5 Relative Growth Rate

The wet weight (g) and total length (TL: cm) of individual fish was measured at the beginning of the experiment (prior to the ramp-up period), and after 6 weeks. Total length was measured using callipers to the nearest 1.0 mm. Relative Growth Rate (RGR) was calculated as the percent increase in wet weight and length.

5.2.6 Body condition

The hepatosomatic index (HI), or relative liver weight, is a common proxy for assessing the energy status of an individual; and is particularly useful for fishes with low fat reserves (Wootton et al., 1978). At the conclusion of the experiments (i.e. after 6 weeks) individuals were euthanised by stunning followed by pithing. Each fish was blotted dry and weighed, and the liver carefully removed and weighed (to the nearest 0.0001g).

5.2.7 Data and Statistical Analysis

Bayesian generalized linear models and Bayesian linear models were used to analyse differences in metabolic rate, feeding rates, feeding selectivity, growth, and body condition of juvenile *Siganus doliatus* reared in different temperature treatments. All analyses were conducted using R (version 3.5.2: R Development Core Team 2016), and Markov Chain

Monte Carlo sampling (Carpenter et al., 2017) were used to fit models in STAN (Stan Development Team, 2018) using the rstanarm package (version 2.17.4: Goodrich et al., 2018). The tidybayes (version 1.0.4: Kay, 2019), broom (version 0.5.1: Robinson & Hayes, 2018) and coda (version: 0.19.2: Plummer et al., 2006) packages were used to summarise model outputs using highest posterior density (HPD) credible intervals with a probability of 95%. Model selection was conducted by comparing Leave One Out Information Criterion values (Vehtari et al., 2017). Where differences in metabolic rate, feeding rates, feeding selectivity, relative growth rate, and body condition were detected, pairwise comparisons were conducted using the emmeans package (version 1.3.3: Lenth, 2019). Strong evidence for an effect was determined if 95% HPD credible intervals did not cross 0 for gaussian models, or 1 for back-transformed non-gaussian models. For all models, trace plots were used to ensure chains were well mixed and converged on a stable posterior, and all rhat values (measure of sampling efficiency) did not exceed 1.1 and the ratio of effective samples versus total samples was > 50%. Priors were determined to be non-informative from diagnostic plots showing that the median and central intervals between posterior and prior were sufficiently wide as to not dictate any trends, without being completely uninformative.

To compare feeding rate and selectivity among temperature treatments, a generalized linear model ‘stan_glm’ was used. The feeding rate model included temperature as a fixed factor. The feeding selectivity model included temperature and algae as fixed factors. Both models were fit with a gamma error distribution with a log-link function. Weakly informative priors were used on all intercepts [~*Normal*(0, 10)], coefficients [~*Normal*(0, 2.5)], and shape [*Exponential*(rate=0.1)] with 5000 iterations, a warmup of 1000, 3 chains and a thinning factor of 3.

To compare resting oxygen uptake and relative growth rate among temperature treatments, individual linear models 'stan_glm' were used. Both models included temperature as a fixed factor, and were fit with a Gaussian error distribution with an identity function. Normality and homogeneity of variance was assessed with Q-Q and box plots. Weakly informative priors were used for all intercepts [~*Normal*(0, 10)] and coefficients [~*Normal*(0, 2.5)], with 5000 iterations, a warmup of 500, 3 chains and a thinning factor of 3.

To compare hepatosomatic index among temperature treatments, a generalised linear model 'stan_glm' was used. Temperature was included as a fixed effect in the model, and was fit with a gamma error distribution with a log-link function. Weakly informative priors were used for all intercepts [~*Normal*(0, 10)], coefficients [~*Normal*(0, 2.5)], and shape [*Exponential*(rate=0.1)] with 5000 iterations, a warmup of 1000, 3 chains and a thinning factor of 3.

5.3 Results

There was strong evidence for an effect of temperature on the metabolic rate, relative growth rate and body condition of *S. doliatus*, but the direction and magnitude of this effect varied for each of the different metrics (Figure 5.1, Table D2).

5.3.1 Resting Oxygen Uptake

There was strong evidence (99-100% probability) of an effect of temperature on the resting oxygen uptake ($MO_{2\ rest}$) of juvenile *S. doliatus*; oxygen uptake was higher in the 28°C, 30°C, and 32°C treatments versus the 26°C treatment. Specifically, $MO_{2\ rest}$ (mean mg O_2 kg^{-1} hr^{-1} [95% Credible Intervals]) was 42%, 38%, and 57% higher in the 28°C (169.0 mg O_2 kg^{-1} hr^{-1} [140.5, 199.0]), 30°C (165.0 mg O_2 kg^{-1} hr^{-1} [138.6, 192]) and 32°C (187.0 [157.5, 220.0])

treatments relative to the 26°C treatment (119.0 mg O_2 kg^{-1} hr^{-1} [91.9, 149.0]), respectively (Figure 5.1a, Table D2).

5.3.2 Feeding Rate

There was moderate evidence (79-89% probability) of an effect of rearing temperature on the feeding rates of juvenile *Siganus doliatus* (Figure 5.1a, Table D2), with feeding rate (mean bites $hour^{-1}$ [95% credible intervals]) being greatest in the 30°C treatment (313 bites $hour^{-1}$ [171, 527]), 36-60% higher than the 26°C (229 bites $hour^{-1}$ [117, 402]), 28°C (210 bites $hour^{-1}$ [103, 378]) and 32°C treatments (192 bites $hour^{-1}$ [104, 328]; Figure 5.1b, Table D2). Feeding rates were similar among individuals reared in the 26°C, 28°C and 32°C treatments.

5.3.3 Relative Growth Rate

There was strong evidence (100% probability) of an effect of temperature on the relative growth rate (% TL: mean [95% credible intervals]) where growth rate was the greatest for individuals in the 28°C temperature treatment (16.2% [10.5, 22.8]), 2.3-fold higher than individuals in the 26°C (4.78% [-1.40, 11.0] and 32°C (4.83% [-1.9, 11.6]) treatments respectively (Figure 5.1c, S1a). (Figure 5.1c, Table D2). A similar pattern was evident for relative growth rate based on changes in wet weight (Figure D2, Table D2).

5.3.4 Body Condition

There was strong evidence (99-100% probability) of an effect of temperature on the Hepatosomatic Index (liver weight: body weight) of *S. doliatus* reared in four different temperature treatments, where HI (mean [95% credible intervals]) was 16-25% lower in the 30°C treatment (0.0127 [0.012, 0.014]), than the 26°C (0.0168 [0.015, 0.019]), 28°C (0.015 [0.014, 0.017]) and 32°C (0.015 [0.013, 0.017]) treatments (Figure 5.1d).

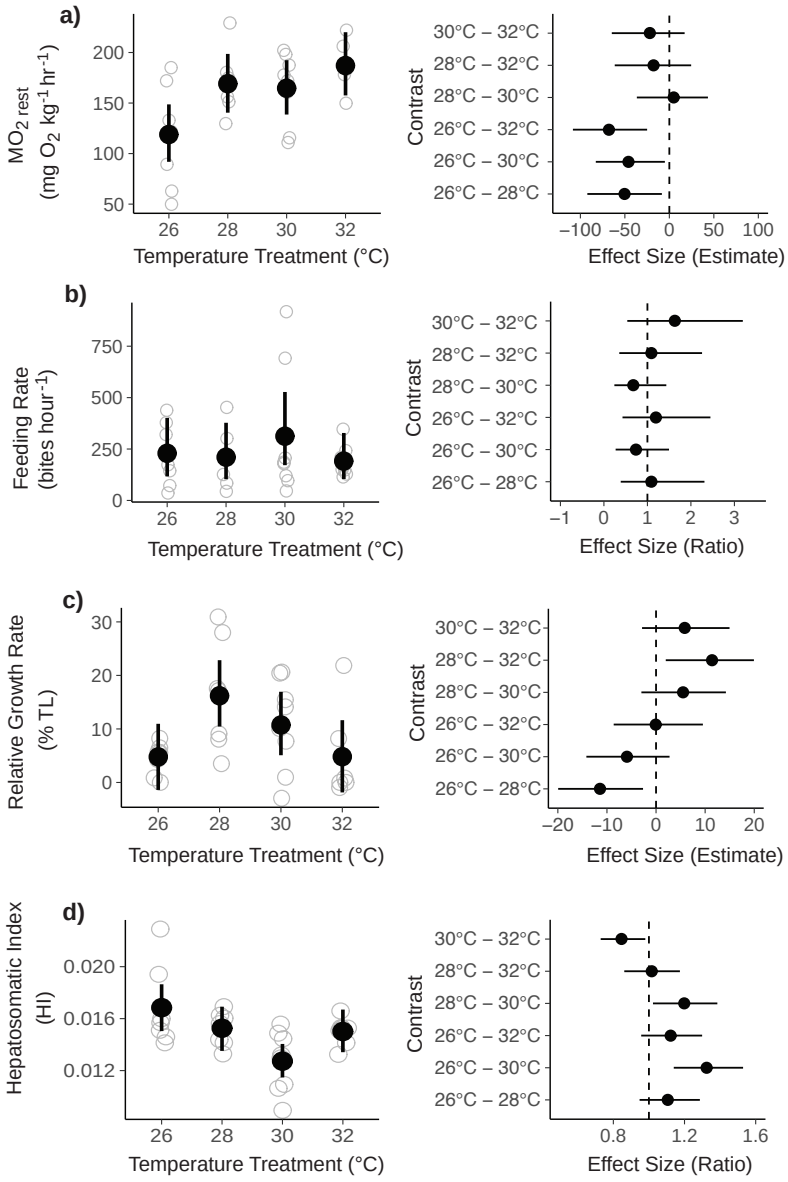

Figure 5.1: Results of Bayesian linear and generalized linear models and effect sizes for associated pairwise contrasts for each parameter for each temperature treatment. a) Feeding Rate (bites * min^{-1}), b) Resting Metabolic Rate ($MO_{2\,rest}$: mg O_2 * kg $fish^{-1}$), c) Relative Growth Rate (% TL) and d) Body Condition (Hepatosomatic Index) of juvenile *Siganus doliatus* reared in four different temperature treatments. Filled circles and lines are mean model estimates ± 95% credible intervals, open grey circles are partial residuals of the models. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that there is an effect of parameter a), b), c), or d) in the temperature that is first listed (to the right of the line) or second listed (to the left of the line). Effect sizes vary between gaussian models ($MO_{2\,rest}$ and Relative Growth Rate) and gamma models (Feeding Rate and Hepatosomatic Index), where gaussian models present the estimated difference between contrasts, and gamma models present the ratio between contrasts.

5.3.5 Feeding Selectivity

Within the 28°C treatment, there was moderate evidence (95% probability) that there were 60% less bites on *Lobophora* (22.2 bites hour^{-1} [8.85, 47.9]), versus *Padina* sp. (55.1 bites hour^{-1} [21.0, 122.2]). Within the 32°C treatment there was moderate evidence (87% probability) that there were 42% less bites per hour on *Lobophora* (29.7 bites hour^{-1} [12.79, 55.2]), versus *Padina* sp. (55.1 bites hour^{-1} [22.5, 100.7]) at 32°C. This preference was negligible (62% and 71% probability) 26°C and 30°C respectively (Figure 5.2, Table D3).

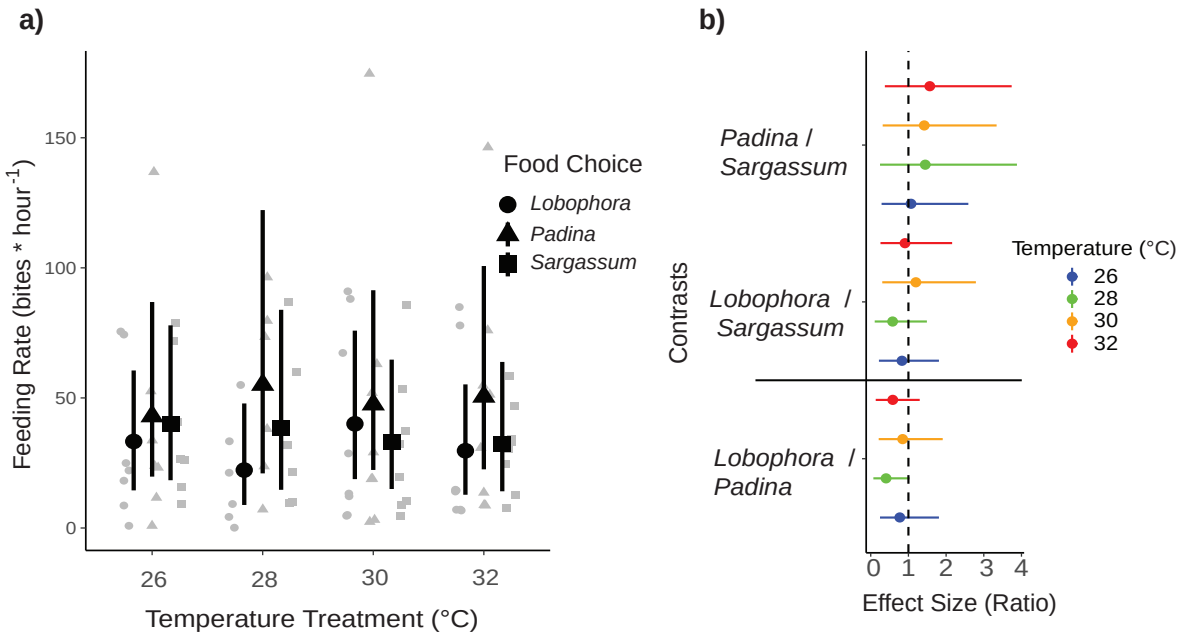

Figure 5.2: a) Results of Bayesian generalized linear models of feeding rate (bites * min^{-1}) on three different macroalgal food choices. Black shapes and lines are mean model estimates ± 95% credible intervals (HPD), grey shapes are partial residuals of the model. Circles indicate bites taken from *Lobophora*, triangles indicate bites taken from *Padina*, and squares indicate bites taken from *Sargassum*. b) The effect sizes for pairwise comparisons of feeding rates of individual fishes offered a choice of three macroalgae. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that feeding rate is greater on the macroalgae that is first listed (to the right of the line) or second listed (to the left of the line).

5.4 Discussion

Understanding the relative responses of metabolism (energy required) and feeding (energy acquired) in relation to temperature is important in predicting the energetic balance of organisms under future environmental change (Iles, 2014). In this study, temperature influenced resting metabolic rate, relative growth rate and body condition of juvenile *S. doliatus*, but the nature of the relationship with temperature differed between metrics. For example resting metabolic rate was highest at 32°C, relative growth was highest at 28°C, and hepatosomatic index (energy reserves) was highest at 26°C, and there was only moderate evidence that feeding rates were highest at 30°C, suggesting a potential temperature-driven metabolic mismatch at temperatures above the summer mean for the region (i.e. 28°C). The increase in metabolic demand was coupled with negligible change in feeding rate and likely energy uptake. This potential energetic deficit was reflected in reduced relative growth and body condition of *S. doliatus* at elevated temperatures. This suggests that feeding rate alone cannot compensate for increased metabolic demand at elevated temperatures, possibly because many herbivores are already nutrient limited due to the relative low nutrient content in plants (Mattson, 1980; Huntly, 1991), and therefore may be limited in their capacity to increase feeding rates.

Here I found that the resting metabolic rate of *S. doliatus* was not matched by changes in feeding rate, where $MO_{2\ rest}$ increased by 57% from 26°C to 32°C, whereas feeding rates remained relatively constant, indicating that metabolic rate (energy required) exceed feeding rates (energy acquired) at elevated temperatures. Similar mismatches where rates of metabolism exceed rates of consumption have also been found in temperate marine invertebrates (Iles, 2014; Lemoine & Burkepile, 2012; Mertens et al., 2015), arctic copepods (Alcaraz et al., 2014) and terrestrial insects (Rall et al., 2010) at elevated temperatures. These

mismatches can result in energy deficits as more energy is allocated to basic cell function and leaving less energy available for growth, reproduction or other activity (Vasseur & McCann, 2005; Lemoine & Burkepile, 2012). For temperate and tropical marine invertebrates and fishes, consumption has been shown to be unlikely to meet metabolic demands when temperatures exceed summer means by 2°C (Lemoine & Burkepile, 2012; Twomey et al., 2012; Alcaraz et al., 2014; Johansen et al., 2014), presumably as many ectotherms are living close to their thermal optima (Sunday et al., 2012). As such, reduced activity and feeding is a viable strategy across taxa to conserve energy at temperatures at or exceeding the summer mean (tropical coral trout: Johansen et al., 2014; Scott et al., 2017, temperate sea star: Twomey et al., 2012). The 30°C treatment in our study is the average summer maximum temperature in the central GBR (AIMS, 2020), suggesting that feeding of juvenile *S. doliatus* might not be able to meet metabolic demand beyond 30°C. This is particularly concerning given these fish recruit to macroalgal beds on the shallow reef flat during the austral summer where temperatures can exceed 32°C in the summer (AIMS, 2020), and climate change is driving increases to mean summer temperatures, and marine heatwaves are expected to increase in frequency and severity (Frölicher et al., 2018; Oliver et al., 2018). Energetic deficits at the juvenile life-history stage are likely to result in reduced somatic growth and development, and ultimately reduced fitness.

As basal metabolic demand increases with increasing temperature, so do the energetic requirements for cell maintenance, leaving less energy available for growth, reproduction and storage (Huey & Kingsolver, 2019). By using juveniles, I have removed the possibility of energy allocation to reproduction. As such, a 57% increase in resting metabolic rate of juvenile *S. doliatus* resulted in a 70% reduction in relative growth at 32°C, and an 11% reduction in relative liver weight, suggesting that feeding alone is not providing enough

energy for processes beyond cell maintenance (i.e. growth) and that energy reserves (i.e. liver storage) are potentially being depleted. Previous studies have also reported reduced or even negative weight gain of coral reef damselfishes at temperatures of +4°C above summer maximum temperatures as a result of elevated metabolic rates (Rummer et al., 2014; Habary et al., 2017), however they did not consider changes energy acquisition or storage. A meta-analysis by Lemoine and Burkepile (2012), found that mismatches where metabolism exceeds consumption often result in reduced growth rates of temperate halibut, salmonids and sturgeon, suggesting that fishes are generally constrained in their capacity to meet increasing metabolic demands through increased food intake (also see: Brett, 1971; Koskela et al., 1997). Therefore, as energetic demands for maintenance increase with increasing temperature, there will be less energy available for activity and growth leading to an overall decline in fitness (Angilletta, 2009; Nilsson et al., 2009). The mismatch between feeding and metabolism found in this study may compromise the growth and development of juvenile *S. doliatus*, leading to smaller individuals, with smaller energetic reserves which may render individuals susceptible predation and lead to decreased survival (Hoey & McCormick, 2004). While changes to feeding rates in this study were negligible with temperature, and suggest that feeding alone does not compensate for increased metabolic demand, potential alternative compensatory mechanisms may be to extend the feeding period (Polunin & Klumpp, 1992), or reduce activity to conserve energy (Johansen et al., 2014; Scott et al., 2017).

Herbivores may compensate for increased energetic demands by increasing the quality or quantity of their food resources (Lubchenco & Gaines, 1981; Huntly, 1991; Sterner & Elser, 2002; Lemoine et al., 2013). The results of this study found little evidence for this where there was negligible change in both feeding rates and feeding selectivity of juvenile *S. doliatus* at increased temperatures. The diet of *S. doliatus* is broad, consisting of filamentous

and corticated green and red algae, and also foliose and leafy brown macroalgae (Hoey et al., 2013), therefore the limited selection (i.e. 3 algal species) from this feeding assay may underestimate the potential for selectivity of *S. doliatus* in the wild. Furthermore the algae offered in this experiment were not grown under elevated temperatures, and the nutritional content and susceptibility to herbivory may vary if grown under such conditions (Chapter 4). Increased temperature increased selectivity (reduced diet breadth) of the generalist herbivorous beetle *P. japonica* when offered the choice of nine plant species, where growth and consumption was greatest on plants with higher nitrogen content (Lemoine et al., 2013). As selectivity of feeding by herbivores is an important determinant of plant community composition (McNaughton et al., 1989; Cyr & Face, 1993), changes to selectivity from generalists to specialists could have implications for the diversity and structure of plant communities into the future.

Due to the relatively short duration of this experiment (i.e. four weeks), the results of this study may be due to acute temperature stress, as four weeks may not account for acclimation of metabolism to temperature. However, as marine heatwaves are becoming more frequent and severe (Frölicher et al., 2018; Oliver et al., 2018), it is still critical to understand the relatively short-term responses to acute temperature stress. Exposure to experimental temperatures for one to two weeks are common for temperature experiments on coral reef fish metabolism (e.g. Barrionuevo & Fernandes, 1998; Nilsson et al. 2009; Rummer et al. 2014). However, the effects of temperature on aerobic performance while still evident, may be reduced under extended exposure to elevated temperatures (i.e. 1-2 weeks: Nilsson et al., 2009; Rummer et al., 2014, vs. 6-8 weeks: Habary et al., 2017; Laubenstein et al., 2019). This suggests that metabolic acclimation to temperature may be possible for tropical fishes, however this varies between species (Schulte et al., 2011; Bernal et al. 2020),

and may occur over multiple generations (Donelson et al., 2012). Furthermore, behavioural responses to temperature are also variable depending on the length of exposure (Abram, et al., 2017). Therefore, the relative rates in thermal acclimation between physiological (i.e. metabolism) and behavioural (i.e. feeding) processes may also influence metabolic mismatch as temperatures continue to increase. Four weeks where temperatures exceed the mean maximum is a critical time for coral reefs, where many fast growing and branching corals begin to die following bleaching (Hughes et al., 2018b). Therefore, understanding the thermal response for this functionally important herbivore species at this critical time point, may provide insights to coral reef recovery following acute temperature stress.

Here, I have provided evidence of a temperature-driven metabolic mismatch resulting in an energy deficit, compromising growth and energy reserves at a critical life-history stage of an ecologically important coral reef fish. As such, reductions in growth and energy storage have been shown to reduce survival in other juvenile coral reef fishes. If reduced fitness (as a result of reduced growth and body condition) ultimately lead to reduced survival of juvenile *S. doliatus* (and potentially other herbivorous taxa), the persistence of herbivorous fish populations may be at risk under future warming. Furthermore, while individual feeding rates were maintained at elevated temperatures, any reductions in population size may also reduce the amount of algal material removed from the reef, therefore releasing algae from top-down control. This could have implications for the future coral-algal balance on coral reefs.

Chapter 6: General Discussion

Increasing global temperatures are the most pervasive climate change stressor, causing shifts to phenology, distribution, behaviour and community composition across terrestrial and marine ecosystems (Bruno et al., 2015; Scheffers et al., 2016; Pecl et al., 2017). The effects of warming are perhaps the most evident on coral reefs, with recent recurrent mass coral bleaching events, resulting in widespread coral mortality (e.g., Hughes et al. 2017a, 2018a,b) and growing concerns that some reefs will be increasingly overgrown with algae (Bellwood et al., 2004; Graham et al., 2015; Hughes et al., 2018b). While large-scale coral mortality often leads to increased algal cover (e.g., Diaz-Pulido & McCook, 2002; Gilmour et al. 2013), and thereby algal production, the likelihood of algal overgrowth will be also dependent on the responses of both algal production and algal consumption to increasing temperatures. This thesis investigated the relative rates of both turf- and macro-algal growth and herbivore feeding rates in response to natural and experimental increases in temperature, and provides evidence that temperature is an important driver of both algal growth and algal consumption on coral reefs. Importantly, algal growth and herbivore consumption responded differently to changing temperature. Both turf- and macro-algal growth initially increased at a lower rate, and peaked at lower temperatures than herbivore feeding rates. These results are in contrast with my hypothesis which predicted that processes driven by photosynthesis (i.e. plants) should be more robust to temperature than processes driven by cellular respiration, following Allen et al. (2005) and Lopez-Urrutia et al. (2006).

In **Chapter 2** I investigated the relative influence of latitudinal variation in temperature versus resource availability in driving feeding rates of three species of nominally herbivorous fish. The consistent positive effect of temperature on the feeding rates of three

herbivorous fish species (*Naso unicornis, Siganus doliatus* and *Ctenochaetus striatus*) with distinct dietary targets, and the variable effect of resource availability suggests temperature is an important driver for feeding rates of herbivorous coral reef fish. I then examined the relative rates of turf algae growth versus feeding rates of eight species of herbivorous fishes with different dietary targets (*N. unicornis, Acanthurus olivaceus, C. striatus, Zebrasoma scopas, Zebrasoma velliferum, Acanthurus nigrofuscus, S. doliatus* and *Siganus corallinus*) in relation to seasonal variation in temperature (**Chapter 3**). I found that while feeding rates of all eight fish species generally increased with temperature (up to 30°C), turf algae growth peaked at 27°C before declining, suggesting a temperature-driven trophic mismatch with consumption exceeding production at elevated temperatures. In **Chapter 4** I used an experimental approach to investigate the effect of temperature on the growth and survival of adult and juvenile *Sargassum*, and found that both adults and propagules are sensitive to prolonged exposure to elevated temperatures (>2°C above ambient), with reduced growth, survival and susceptibility to herbivory. In **Chapter 5** I also used an experimental approach to investigate the effect of temperature on the metabolic rate, feeding rate, growth and body condition of juvenile *S. doliatus*, a common herbivorous coral reef fish. I found that exposure to temperatures exceeding summer maximums (32°C) increased resting metabolic rate, but feeding rates did not increase to compensate for increased metabolic demand. Growth and body condition also decreased at elevated temperature suggesting a potential energy deficit at elevated temperatures.

Combining the responses of both algal growth and feeding rates of herbivorous fishes from the individual chapters shows a general decrease in algal growth at temperatures > 27°C (Figure 6.1a-c) and a general increase in feeding rates between the winter and summer temperatures (23°C -30°C: Figure 6.1d-k). This mismatch between algal growth and

herbivore feeding in response to temperature suggests that the likelihood of algal overgrowth on coral reefs into the future may be lower than previously assumed, provided the responses of fishes and algae examined in this thesis are representative of the broader community.

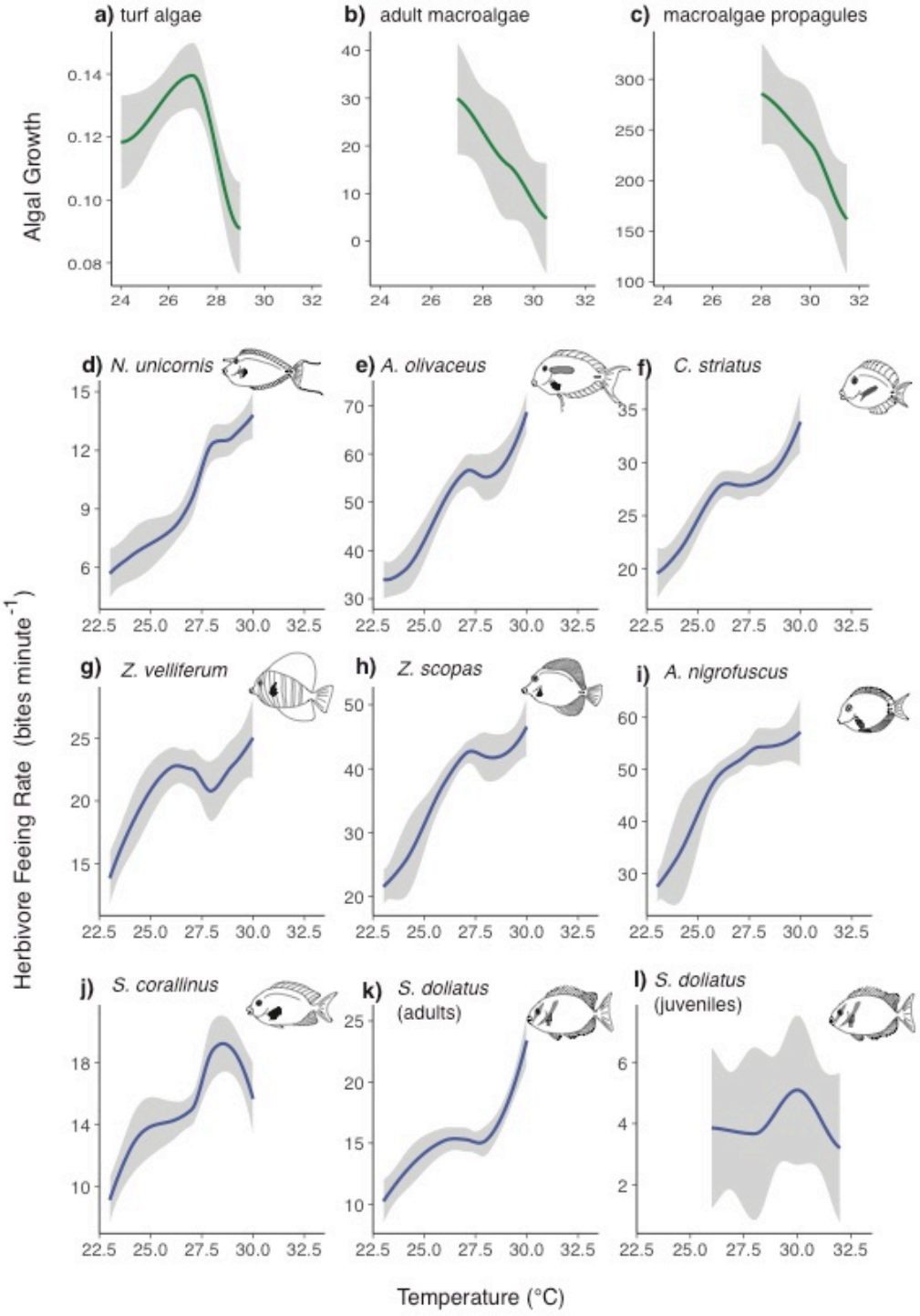

Figure 6.1: The effect of temperature on the growth of a) turf algae, b) adult macroalgae c) macroalgae propagules and the feeding rates of eight herbivorous fishes on the Great Barrier Reef (d-l) . Turf algal growth data is from Chapter 3, macroalgae growth data are all adult *Sargassum* spp. combined from Chapter 4, and propagule data is from Chapter 4, feeding data of adult herbivorous fishes (d-k) are combined across latitude (Chapter 2) and season (Chapter 3) and juvenile *S. doliatus* (l) is data from Chapter 5. All raw data are fit with a Loess smoother ± SE.

The different responses between algal growth and consumption found in this thesis suggests that there is may be a trophic mismatch as temperature increases, whereby it is likely that consumption will exceed algal growth (Figure 6.2a). Of the three potential mismatches in algal production and consumption under elevated temperatures described in Chapter 1 (Dell et al., 2014, Figure 1.3), the results of this thesis suggest that this mismatch is driven by a combination of slower rates of increase, and lower thermal optima of algal growth versus herbivore consumption (Figure 1.3c,d). Both turf- and macro-algal growth peaked at a lower temperature (~27°C), and I did not identify a peak in fish feeding rates, as they continued to increase in summer when temperatures were the highest (30°C: Figure 6.1 a-l). However, the rates of increase between algal growth and herbivore feeding as a result of temperature differed. For example, comparisons among seasons showed that a ~3°C increase in temperature (i.e. winter: 24°C to spring: 27°C) resulted in relatively small (12%) increase in turf algae growth, especially compared to the larger (50%-146%) increases in herbivorous fish feeding rates over the same temperature range (Figure 6.1a, d-k). Moreover, at summer temperatures a decrease in the growth of turf-algae, and propagules and adult thalli of the macroalgae *Sargassum* was evident (Chapters 3 and 4). These declines in algal growth coupled with increased consumer pressure during the summer, may lead to net reductions in algal biomass under elevated temperatures (Figure 6.2b). These results are consistent with metabolic scaling theory, which predicts that processes driven by photosynthesis will respond to temperature at a relatively slower rate than processes driven by cellular respiration (Allen et al., 2005; López-Urrutia et al., 2006). Similar trophic mismatches have been documented in marine invertebrates in temperate pelagic (O'Connor et al., 2009), intertidal (Mertens et al., 2015) and subtidal kelp (Gutow et al., 2016) ecosystems, where consumption can exceed production up to 2.5-fold due to small increases in temperature resulting in decreased algal

biomass, and potential food limitation for consumers. Increased consumption paired with reduced algal growth may accelerate the decline in algal biomass on coral reefs, giving rise to novel system both low in coral and macroalgal cover into the future (Fulton et al., 2019).

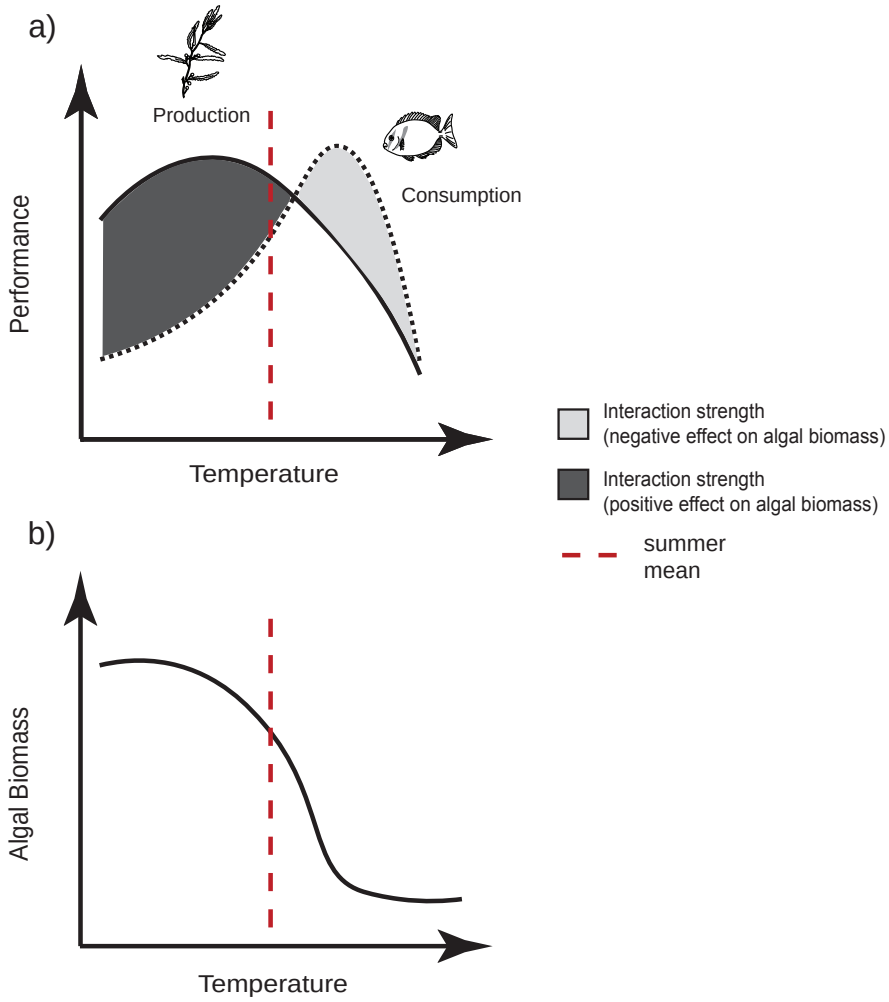

Figure 6.2: Conceptual diagram for summarising the trophic mismatch between herbivore consumption and algal growth observed in this thesis, and the potential outcome for algal biomass on coral reefs.

While there was generally a positive relationship between environmental temperature and feeding rates of herbivorous fishes, there was some evidence that this may come at a physiological cost to individual fish (Figure 6.3). In Chapter 5, I found that when juvenile *S. doliatus* were exposed to elevated temperatures (28°C -32°C) their resting metabolic rate

increased, but their feeding rate remained unchanged suggesting they had limited capacity to compensate for the increased metabolic demand (Figure 6.3). Further, their growth and body condition was suppressed at elevated temperatures. Such a metabolic mismatch could ultimately lead to a 'metabolic meltdown' if organisms cannot obtain enough energy from food to compensate for increased metabolic demand from prolonged exposure to elevated temperatures, and thereby accelerating the negative effects (i.e. physiological costs) of climate change (Huey & Kingsolver, 2019). The reduced susceptibility of macroalgae cultured under elevated temperatures (Chapter 4), may further limit energy gains under such conditions. If these findings are representative of other herbivorous taxa, energetic deficits could lead to smaller individuals, at risk of increased predation and reduced survival (Hoey & McCormick, 2004), therefore reducing the replenishment of herbivore populations. While not assessed in this thesis, energetic deficits may reduce reproduction in adults (e.g. Henderson et al., 1996). Both reduced herbivore populations, and populations comprised of smaller individuals may reduce overall grazing pressure of algae on coral reefs, which may release algal communities from top-down control, leading to a potential shift to an algal-dominated state (e.g. Hughes et al. 2007). As exposure to current summer maximum temperatures are predicted to increase, and exposure to winter minimums are predicted to decrease on coral reefs (Lough, 2012), understanding the duration that compromised individuals can withstand exposure to elevated temperatures, and/or the ability to acclimate or adapt to such stressors, will be critical in predicting how long the ecological functional role of herbivorous fishes may be maintained into the future.

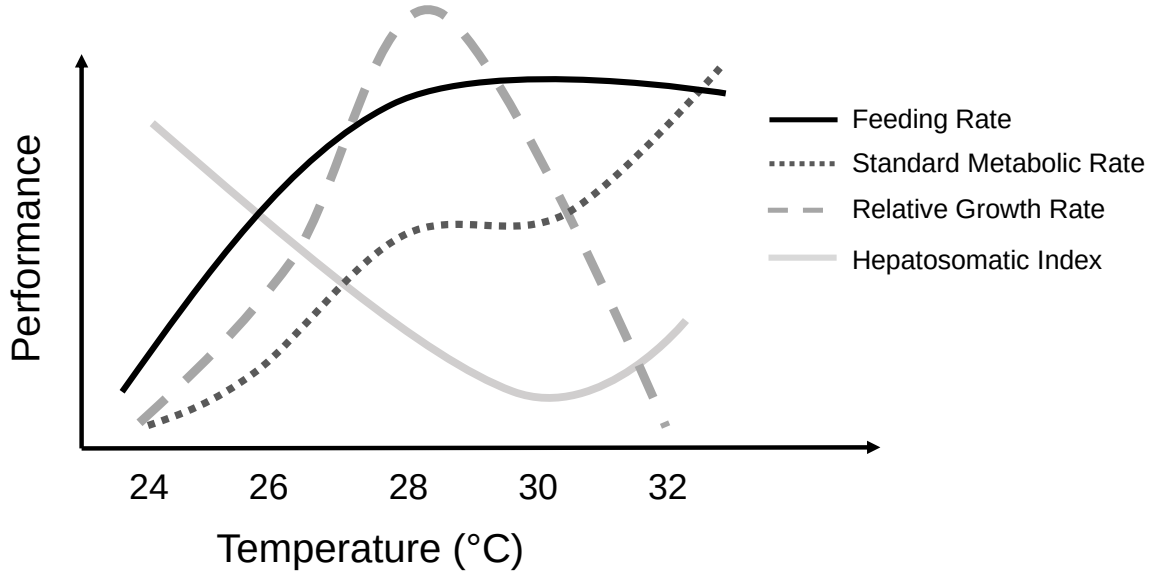

Figure 6.3: Conceptual diagram summarising the metabolic mismatch between individual consumption, standard metabolic rate, growth and body condition (hepatosomatic index) of juvenile *S. doliatus* in Chapter 5 in relation to increases in environmental temperature.

There were differences in the thermal response of feeding rates between adult fishes in the field across latitude and season (Chapters 2 and 3) and juvenile *S. doliatus* in experimental conditions (Chapter 5). Specifically, while adult fishes in the field increased their feeding rates by 25-140% under relatively small increases (~2-3°C) in temperature, juvenile fishes in experimental conditions exhibited negligible differences in feeding rates across a 6°C range in experimental temperatures. This may be due to the differences in energetic requirements between adult and juvenile fishes, where juveniles may have increased metabolic demand for somatic growth and development, potentially rendering this age class more vulnerable to temperature-driven metabolic mismatch (Huey & Kingsolver, 2019). However, juvenile *S. doliatus* among other tropical herbivorous fishes, recruit to the *Sargassum* beds on the reef flat (Tang et al., 2020), where temperatures are likely more variable than the reef slope (Harbourne, 2013), which may broaden the thermal tolerance

range of this life-history stage (Sunday et al., 2012), or may lead to developmental plasticity in the thermal response (Donelson et al. 2011). While ontogenetic shifts in thermal tolerance, and differences in energetic budgets between adults and juveniles may explain differences in the response of feeding rates as a result of temperature in this thesis, nutritional quality of resources may also be a likely contributor to this variation (Clements et al., 2009). Due to the low nitrogen content in plants, herbivores are often nitrogen limited and will either increase food quantity or quality to gain adequate nitrogen (Mattson, 1980; Huntly, 1991). As such, experimental juvenile *S. doliatus* was fed a limited and controlled diet, compared to the dietary resources available to adult fishes observed in the field. Furthermore, dietary resource quality may also vary spatially and temporally, which may also influence feeding rates across latitude and season (Clements et al., 2009). It is therefore likely that a combination of both energetic and nutritional requirements may differentially influence feeding rates between adults and juvenile herbivorous fishes. Understanding energetic budgets between both adults and juveniles under future change may provide insight into the sensitivity of each life-history stage to future metabolic mismatch, and warrants future investigation.

The outcome of future mismatches will also be dependent on the ability of each trophic level to acclimate or adapt to future conditions. It has been suggested that due to the narrow thermal tolerance range of tropical ectotherms, the potential to acclimate to increased temperatures may be small (Janzen 1967; reviewed by Huey et al., 2012). Marine macroalgae are sessile and cannot move to more favourable thermal environments, and so must rely on physiological mechanisms driven by changes to gene expression: phenotypic plasticity or genetic adaptation (King et al., 2019). Such changes can lead to differences in thermal tolerances in macroalgae (i.e. adaptive capacity e.g. *Undaria pinnatifida* and *Egregia menziesii*; Henkel & Hofmann, 2008), or to different morphologies among different

populations (phenotypic plasticity: e.g. *Hormosira banksia*; Clark et al., 2018). Adaptation is favoured over epigenetic responses for macroalgae, due to the limited gene flow between populations, and evidence of distinct thermal ecotypes among widespread distributions (Reusch, 2014; Wernberg et al., 2018; King et al., 2019).

Coral reef fishes have also been shown to acclimate to elevated temperatures (+3°C) within one generation via developmental plasticity (Donelson et al., 2011), or over multiple generations via transgenerational acclimation (Donelson et al., 2012). Current research on coral reef fishes however, focusses mainly on epigenetics and phenotypic plasticity (e.g. Donelson et al., 2011; Donelson et al., 2012; Spinks et al., 2019), likely due to logistical constraints with adaptive genetic selection occurring over many generations. However, it has been suggested that phenotypic plasticity and range shifts may be a more viable option (rather than selective adaptation) for many mobile organisms to cope with warming (Merilä, 2012; Kelly, 2019), but would have to occur within each generation (Donelson et al., 2019). Moreover, mobile organisms also have the advantage of behaviourally compensating from thermal stress, i.e. the Bogert effect (e.g. Stellatelli et al., 2018), which may further complicate adaptive selection (Kelly, 2019). Therefore, predicting relative rates of acclimation and adaptation in either trophic group is difficult (Kelly, 2019). Given the high generational turnover of algae relative to fishes, it can be assumed that adaptation to thermal stress, if possible, may occur faster for algae versus fishes. However, the net outcome to future trophic mismatch will be dependent on the rates of acclimation and adaptation between consumer and resource as temperatures continue to increase.

Ultimately, if temperature increases beyond the range which an organism can tolerate, or the rate of warming exceeds rates of acclimation or adaptation, marine organisms will have

to seek thermal refuge at greater depths (MacDonald et al., 2016), expand their range poleward (Vergés et al., 2016; Pecl et al., 2017; Booth et al., 2018), reduce activity (Johansen et al., 2014; Scott et al., 2017), or die (Habary et al., 2017). Local extirpation of populations of macroalgae have been observed worldwide following abrupt heatwaves and repeated recruitment failures (Prince, 1980; McCourt, 1984; Smale & Wernberg, 2013; Bates et al., 2014; Thomsen et al., 2019), while chronic increases in temperature have led to poleward range shifts to cooler waters (e.g. Lima et al., 2007; Tanaka et al., 2012). Given declines in growth (-17-49%) and declines in survival (-84%) for the tropical *Sargassum* observed in this thesis, it is likely that prolonged exposure to temperatures at or above current summer maximums will cause a decrease in abundance and ultimately a range contraction at the warm boundary of its range. Local extinction of and poleward retraction of tropical macroalgae may result in altered macroalgal communities (Smale & Wernberg, 2013), reduced habitat complexity (Fulton et al., 2019), resulting in altered ecosystem function (Wernberg et al., 2013). Range shifts of tropical herbivorous fishes (f. Siganidae, f. Acanthuridae) have also been observed at the higher latitude of their distributional range (Nakamura et al., 2013; Vergés et al., 2014, 2016; Basford et al., 2016; Wernberg et al., 2016; Zarco-Perello et al., 2017), leading to the 'deforestation of temperate algal forests' on the east and west coasts of Australia (Vergés et al., 2014; Wernberg et al., 2016; Zarco-Perello et al., 2017), and in Japan (Kumagai et al., 2018) as tropical herbivorous fishes invade and overgraze temperate habitat-forming macroalgae (Vergés et al., 2016). In Chapter 5, I found some evidence for reduced individual fitness (i.e. increased metabolic demand, reduced growth, reduced body condition) of juvenile *Siganus doliatus* exposed to 32°C for 5 weeks, suggesting that living at summer maximum temperatures is energetically costly and may not be sustainable over longer timeframes. While the range expansion of herbivores at the high latitude edge of their range is becoming increasingly studied, threat of local extirpation, or range contraction at the lower

latitude of their distribution has received less attention. The results of this study suggest that if temperatures increase beyond 32°C, or time spent at summer maxima (32°C) increases, could lead to a range contraction of herbivorous fishes (at least *S. doliatus*) at the low latitude limit of their distribution.

The consistent response to temperature for algal growth and herbivore consumption across the four data chapters of this thesis suggest a likely temperature-driven trophic mismatch, which may have implications for algal biomass and proliferation into the future. However, this projected mismatch is assuming that the responses observed in this thesis are representative of the broader coral reef community. Furthermore, herbivore feeding is also largely influenced by the nutrient content and tissue quality of the targeted algal resource (Huntly, 1991; Clements et al., 2009) which I did not assess. While the consistent pattern in feeding rates of different functional feeders across latitude and season suggests a strong influence of environmental temperature, there also may be a likely interaction between the quality of resources over these spatial and temporal scales (Clements et al., 2009). Lastly, I only assessed one of many trophic interactions on coral reefs. Herbivores themselves are resources to higher level consumers, and understanding how these interactions may shift will also be important in determining changes to top down control of plant communities (Schmitz, 2008). Given that coral reef ecosystems are highly complex, understanding how multi-trophic systems may shift into the future is critical.

Ocean warming is one of the most pervasive threats facing coral reefs, already causing widespread coral mortality, with concerns that coral reefs may be overgrown by macroalgae (Bellwood et al., 2004; Graham et al., 2015). This threat is dependent on the outcome of increasing temperature to algae-fish interactions, a critical process on coral reefs

which mitigates algal dominance. The results of this thesis suggest that this threat may be less likely than previously assumed, where algae was more negatively impacted by temperature than herbivores. Therefore, it may be possible that instead of moving from a coral-dominated, to a macroalgal-dominated state, novel and structurally simple systems may arise, depauperate in both coral and macroalgae. However, it remains to be seen how epigenetic processes and adaptation may alter any potential trophic mismatch into the future. Consequently, it is imperative to understand both the short term (acute) and long term (chronic) effects of temperature to the outcome of algae-fish interactions. The results of this thesis have provided new insights on the relative thermal dependence between consumers and producers on coral reefs, increasing our understanding of how algae-fish interactions may shift into the future, and how this may impact coral reef ecosystem structure.

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Appendix A: Supporting information for Chapter 2

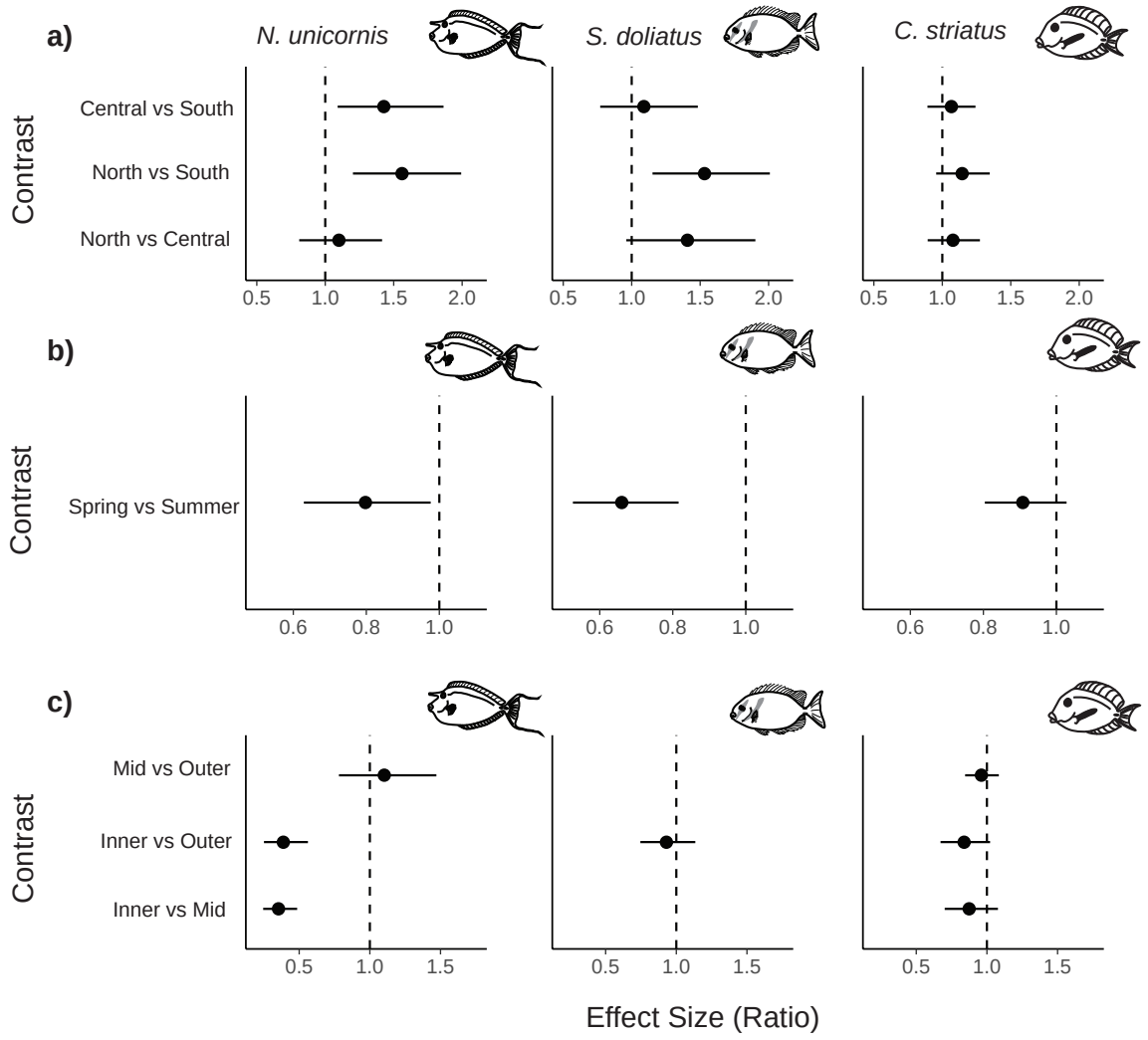

Figure A1: The effect sizes of pairwise contrasts of the feeding rates of *Naso unicornis*, *Siganus doliatus* and *Ctenochaetus striatus* for each a) latitude, b) season and c) shelf position. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that feeding rate is greater in the latitude/season/shelf position that is first listed (to the right of the line) or second listed (to the left of the line)

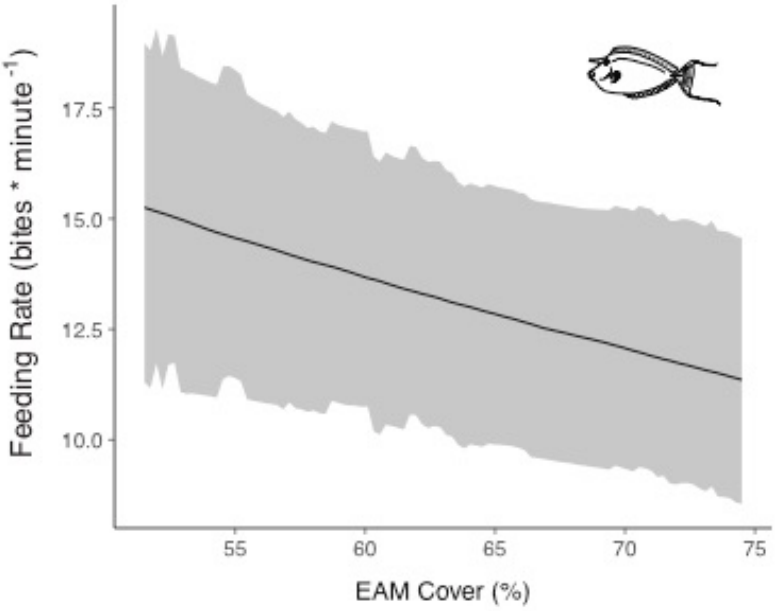

Figure A2: The relationship between EAM Cover (%) and Feeding Rate (bites minute^{-1}) of *Naso unicornis* between austral spring and summer in the northern GBR. The black line is the result of the Bayesian generalized mixed effects model, and grey ribbons are the 95% Credible Intervals.

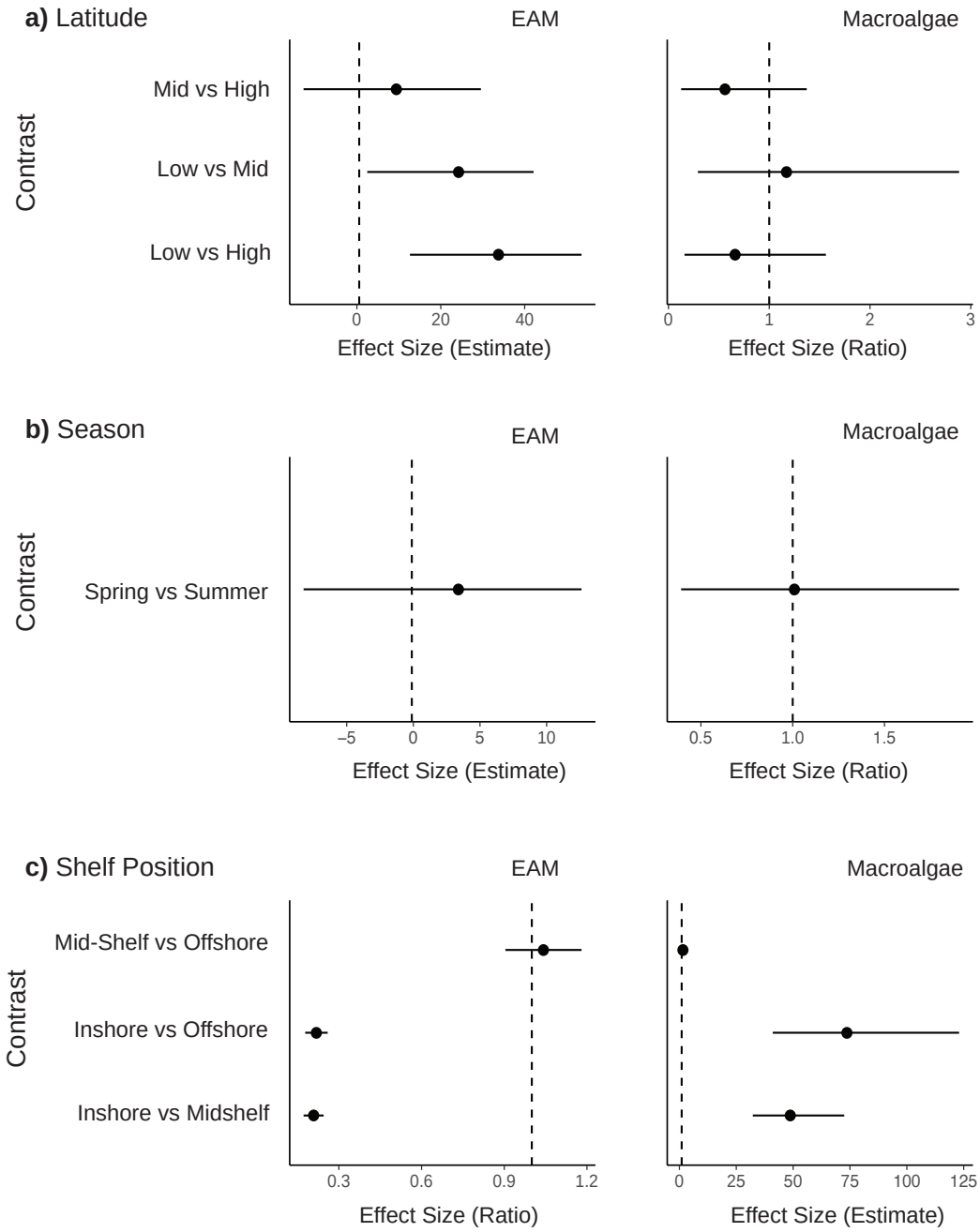

Figure A3: The effect sizes for pairwise comparisons for the cover of EAM and macroalgae (a) across three latitudes along the GBR, (b) between two seasons in the low latitude sites of the GBR (c) across three shelf positions across the continental shelf of low latitude sites of the GBR. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that macroalgae or EAM cover is greater in the latitude/season/shelf position that is first listed (to the right of the line) or second listed (to the left of the line).

Proportion of bites

The proportion of total bites on EAM versus macroalgae differed between the inner-shelf and mid-shelf reefs for all species. On average, 62% of total bites of *N. unicornis*, 27% of total bites of *S. doliatus* and 14% of total bites of *C. striatus* targeted macroalgae in the inner-shelf reefs compared to the 1% and 0% of total bites targeting macroalgae in the mid-shelf and outer-shelf reefs across all species (Figure A4). In the mid-shelf reefs, 98-99% of all bites targeted EAM from all species. In the outer-shelf reefs, 8% of total bites of *C. striatus* targeted crustose coralline algae (CCA), 3% targeted macroalgae, and 88% targeted the EAM (Figure A4c).

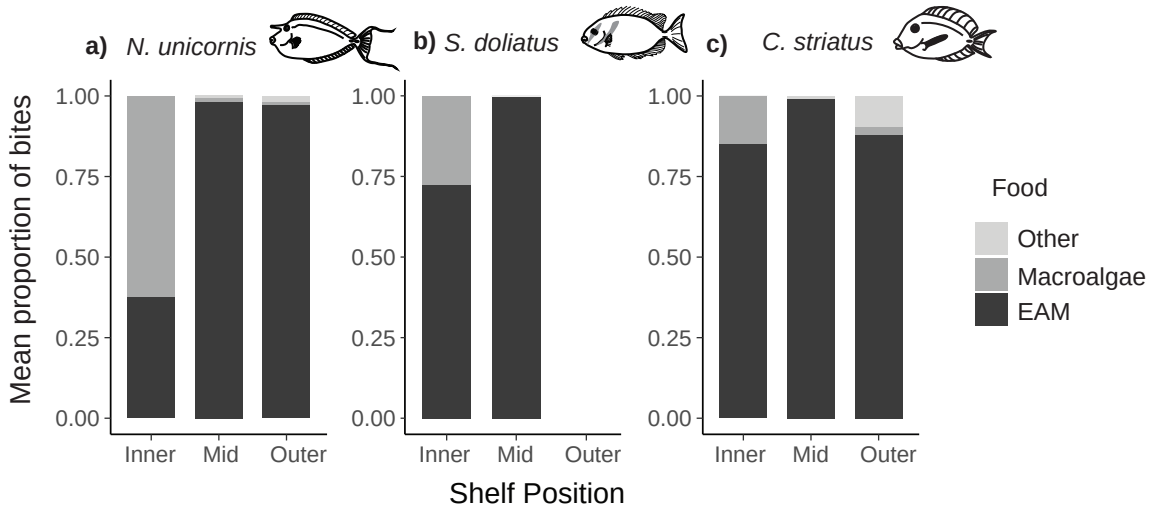

Figure A4: Mean proportion of total bites taken by a) *N. unicornis*, b) *S. doliatus* and c) *C. striatus* and from difference resources at different reefs across the continental shelf.

The effect of body size on feeding rate

There was also evidence for a the effect of negative correlation between feeding rate and total length of *N. unicornis* across latitude, season and the continental shelf and a positive correlation between feeding rate and total length of *S. doliatus* across latitude, season and the continental shelf (Figure A5a, b, Tables A2, A3, A4). There was weak evidence for a negative correlation between feeding rate and total length of *C. striatus* across latitude, season and the continental shelf (Figure A5c, Tables A2, A3, A4).

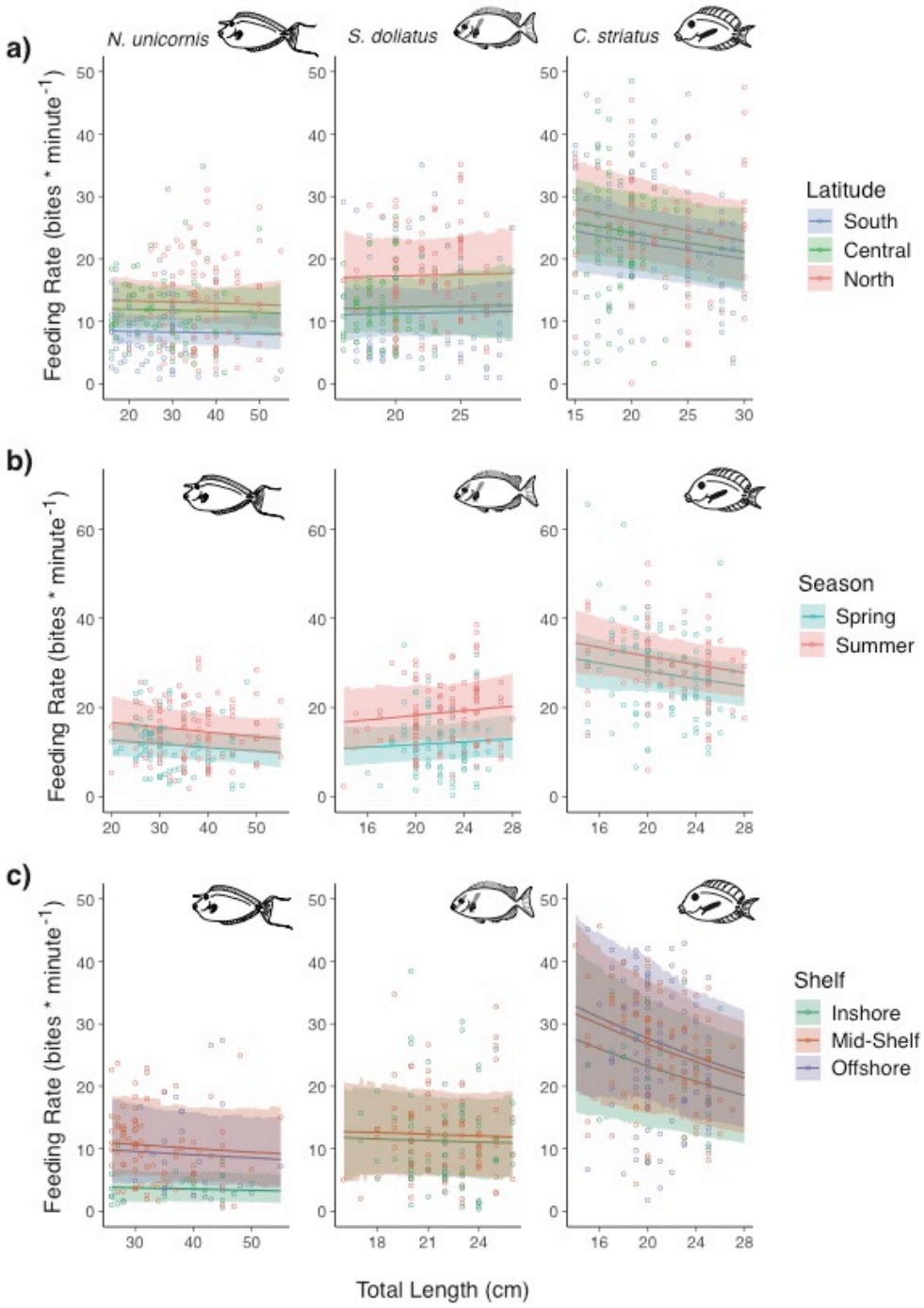

Figure A5: Feeding rates (Bites minute^{-1}) of three herbivorous fishes of different sizes (Total Length (cm)) across (a) three latitudes across the GBR, (b) two seasons at the mid-shelf reefs in the northern sites of the GBR and (c) three continental shelf positions in the in the low latitude sites of the GBR. Lines and ribbons are estimates of Bayesian mixed models ± 95% Credible Intervals, points are partial residuals of the model.

Table A1: Results of comparisons of estimated Leave One Out Information Criterion (LOOIC) and Expected Log Predictive Density LOOIC (elpd LOO) values and standard errors (SE) comparing models with EAM Cover (%) versus models with Latitude as fixed factors for feeding rates across three latitudes along the GBR. Continuous predictors (Total Length (TL) and EAM Cover) have been centred and scaled. The best fit model is determined by the lowest LOOIC value and indicated in bold font.

Species	Fixed Effects	elpd_loo (SE)	LOOIC (SE)
N. unicornis	EAM Cover + TL	-796 (10)	1592 (21.8)
	Latitude + TL	**-793 (11.1)**	**1586.5 (22.3)**
S. doliatus	EAM Cover + TL	-900.9 (11.2)	1801.9 (22.4)
	Latitude + TL	**-898.5 (11.2)**	**1797 (22.4)**
C. striatus	EAM Cover + TL	-935.1 (10.5)	1870.8 (20.8)
	Latitude + TL	**-935.4 (10.4)**	**1870.8 (20.8)**

Table A2: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of three herbivorous fishes across three latitudes along the GBR. Results are on the log link scale.

Species	**Term**	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
a) *N. unicornis*	(Intercept)	2.56	0.12	2.31	2.79	1.00	1544
	Latitude: Mid	-0.08	0.14	-0.35	0.21	1.00	1503
	Latitude: South	-0.44	0.13	-0.68	-0.18	1.00	1535
	Size	0.00	0.01	-0.01	0.01	1.00	1506
	Shape	2.76	0.24	2.33	3.25	1.00	1731
	Sigma	0.06	0.11	0.00	0.23	1.00	1335
	mean_PPD	15.65	1.01	13.81	17.68	1.00	1569
	log-posterior	-915.36	3.50	-921.91	-908.63	1.00	1302
b) *S. doliatus*	(Intercept)	2.84	0.15	2.55	3.13	1.00	1581
	Latitude: Mid	-0.33	0.17	-0.65	0.01	1.00	1704
	Latitude: High	-0.42	0.14	-0.69	-0.15	1.00	1486
	Size	0.00	0.02	-0.03	0.03	1.00	1502
	Shape	2.24	0.19	1.87	2.60	1.00	1791
	Sigma	0.15	0.17	0.00	0.40	1.00	1594
	mean_PPD	15.65	1.01	13.81	17.68	1.00	1569
	log-posterior	-915.36	3.50	-921.91	-908.63	1.00	1302
c) *C. striatus*	(Intercept)	3.24	0.13	2.99	3.51	1.00	1798
	Latitude: Mid	-0.08	0.09	-0.25	0.09	1.00	1759
	Latitude: High	-0.13	0.09	-0.30	0.04	1.00	1701
	Size	-0.01	0.01	-0.03	0.00	1.00	1523
	Shape	6.48	0.56	5.47	7.59	1.00	1444
	Sigma	0.10	0.13	0.00	0.28	1.00	1739
	mean_PPD	28.29	1.02	26.25	30.30	1.00	1772
	log-posterior	-957.13	3.60	-964.26	-950.76	1.00	1487
	mean_PPD	11.26	0.63	9.97	12.41	1.00	1687
	log-posterior	-813.04	3.94	-820.44	-805.25	1.00	1171

Table A3: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of three herbivorous fishes at two different seasons at the mid-shelf reefs in the northern GBR. Results are on the log link scale.

Species	**Term**	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
a) *N. unicornis*	(Intercept)	2.45	0.12	2.18	2.69	1.00	1553.00
	Season: summer	0.23	0.11	0.00	0.43	1.00	1708.00
	EAM	-0.10	0.05	-0.18	-0.01	1.00	1844.00
	Total Length	-0.07	0.04	-0.15	0.02	1.00	1600.00
	shape	3.19	0.31	2.60	3.79	1.00	1569.00
	Sigma	0.07	0.12	0.00	0.21	1.00	1712.00
	mean PPD	12.93	0.76	11.48	14.41	1.00	1931.00
	log posterior	-658.04	3.22	-664.50	-652.53	1.00	1709.00
b) *S. doliatus*	(Intercept)	2.49	0.18	2.11	2.83	1.00	1472.00
	Season: summer	0.42	0.11	0.20	0.64	1.00	1731.00
	EAM	-0.05	0.04	-0.14	0.03	1.00	1677.00
	Total Length	0.03	0.04	-0.05	0.11	1.00	1779.00
	shape	3.89	0.40	3.16	4.68	1.00	1728.00
	Sigma	0.17	0.20	0.00	0.50	1.00	1497.00
	mean PPD	17.23	0.93	15.42	19.05	1.00	1659.00
	log posterior	-668.51	3.59	-675.50	-661.94	1.00	1159.00
c) *C. striatus*	(Intercept)	3.23	0.05	3.14	3.33	1.00	1597.00
	Season: summer	0.09	0.06	-0.03	0.22	1.00	1763.00
	EAM	0.00	0.03	-0.05	0.06	1.00	1650.00
	Total Length	-0.04	0.03	-0.10	0.02	1.00	1789.00
	shape	9.06	0.99	7.15	10.98	1.00	1868.00
	Sigma	0.01	0.01	0.00	0.02	1.00	1707.00
	mean PPD	26.43	0.99	24.45	28.32	1.00	1649.00
	log posterior	-581.75	2.78	-587.18	-576.92	1.00	1528.00

Table A4: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of three herbivorous fishes across the continental shelf. Results are on the log link scale.

Species	**Term**	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
a) *N. unicornis*	(Intercept)	1.31	0.34	0.60	1.98	1.00	1292
	Shelf: mid	1.03	0.17	0.67	1.35	1.00	1557
	Shelf: outer	0.94	0.21	0.53	1.32	1.00	1562
	Size	-0.01	0.01	-0.02	0.01	1.00	1824
	shape	2.04	0.23	1.59	2.46	1.00	1735
	Sigma	0.35	0.62	0.00	1.45	1.00	1264
	Mean PPD	10.12	0.89	8.49	11.95	1.00	1953
	log-posterior	-442.72	2.74	-447.97	-437.78	1.00	1434
b) *S. doliatus*	(Intercept)	2.43	0.29	1.81	2.96	1.00	1307
	Shelf: mid	0.07	0.11	-0.14	0.29	1.00	1513
	Size	-0.01	0.02	-0.05	0.04	1.00	1687
	shape	2.38	0.24	1.95	2.88	1.00	1484
	Sigma	0.34	0.69	0.00	1.24	1.00	1339
	Mean PPD	12.51	0.90	10.77	14.26	1.00	1597
	log-posterior	-567.03	2.69	-572.38	-562.24	1.00	1395
c) *C. striatus*	(Intercept)	3.13	0.22	2.70	3.53	1.00	1830
	Shelf: mid	0.13	0.11	-0.09	0.34	1.00	3672
	Shelf: outer	0.17	0.11	-0.03	0.39	1.00	3723
	Size	-0.03	0.01	-0.05	-0.01	1.00	4406
	shape	4.83	0.42	4.08	5.70	1.00	4341
	Sigma	0.17	0.59	0.00	0.63	1.00	2383
	Mean PPD	27.25	1.16	25.04	29.42	1.00	4420
	log-posterior	-947.52	2.92	-953.12	-942.25	1.00	1842

Table A5: Results of Bayesian hierarchical models with gaussian (EAM) and poisson (Macroalgae) distributed errors for the percent cover of EAM and macroalgae across three latitudes along the GBR. Results are on the log link scale.

Resource	**Term**	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
EAM	(Intercept)	60.66	7.30	46.54	75.15	1.00	2327.0
	Latitude: Mid	-24.06	10.30	-43.97	-3.11	1.00	2373.0
	Latitude: High	-33.73	10.44	-55.02	-13.12	1.00	2183.0
	sigma	10.59	1.52	7.94	13.70	1.00	2269.0
	Sigma	137.47	114.88	0.04	338.54	1.00	1975.0
	Mean PPD	41.30	2.54	36.49	46.57	1.00	2341.0
	log-posterior	-160.31	3.59	-167.73	-153.98	1.00	1704.0
Macroalgae	(Intercept)	0.11	0.38	-0.70	0.82	1.00	2324.0
	Latitude: Mid	-0.17	0.54	-1.27	0.82	1.00	2285.0
	Latitude: High	0.39	0.51	-0.61	1.40	1.00	2112.0
	Sigma	0.21	0.29	0.00	0.74	1.00	1988.0
	Mean PPD	1.34	0.28	0.83	1.89	1.00	2347.0
	log-posterior	-64.97	3.14	-71.19	-59.47	1.00	2039.0

Table A6: Results of Bayesian hierarchical models with gaussian (EAM) and poisson (Macroalgae) distributed errors for the percent cover of EAM and macroalgae between two seasons at the low latitude, mid-shelf reefs of the GBR. Results are on the log link scale.

Resource	**Term**	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
EAM	(Intercept)	64.94	6.90	48.43	76.85	1.00	2046.0
	Season: summer	-3.18	5.39	-13.57	7.37	1.00	2492.0
	sigma	13.12	2.09	9.21	17.23	1.00	2333.0
	Sigma	114.65	265.31	0.00	451.21	1.00	2106.0
	Mean PPD	63.50	3.85	56.13	71.28	1.00	2378.0
	log-posterior	-110.71	2.45	-115.37	-106.76	1.00	1830.0
Macroalgae	(Intercept)	0.11	0.38	-0.65	0.80	1.00	2371.0
	Season: summer	0.00	0.37	-0.79	0.69	1.00	2811.0
	Sigma	0.21	0.60	0.00	0.89	1.00	2550.0
	Mean PPD	1.17	0.31	0.58	1.75	1.00	2720.0
	log-posterior	-40.06	2.00	-43.98	-36.81	1.00	2767.0

Table A7: Results of Bayesian hierarchical models with poisson distributed errors for the percent cover of EAM and macroalgae across three shelf positions across the continental shelf of the northern GBR. Results are on the log link scale.

Resource	**Term**	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
EAM	(Intercept)	2.61	0.08	2.46	2.76	1.00	2191.0
	Shelf: Mid	1.56	0.09	1.39	1.74	1.00	2176.0
	Shelf: Outer	1.52	0.09	1.34	1.71	1.00	2200.0
	Sigma	0.01	0.01	0.00	0.02	1.00	2134.0
	Mean PPD	48.62	1.38	46.12	51.37	1.00	2397.0
	log-posterior	-215.36	3.92	-222.95	-208.42	1.00	1973.0
Macroalgae	(Intercept)	4.32	0.06	4.22	4.43	1.00	2429.0
	Shelf: Mid	-3.88	0.19	-4.25	-3.51	1.00	2435.0
	Shelf: Outer	-4.31	0.26	-4.78	-3.81	1.00	2558.0
	Sigma	0.01	0.03	0.00	0.04	1.00	1953.0
	Mean PPD	24.19	0.97	22.27	26.13	1.00	2253.0
	log-posterior	-133.81	3.40	-140.73	-127.50	1.00	2202.0

Statistical Analysis – Benthic and Herbivore Communities

To visualise any variation in herbivorous fish assemblages or benthic communities among sites or seasons individual non-metric Multi-Dimensional Scaling (nMDS) analysis were performed using the vegan package in R (version 2.5.4: Oksanen et al., 2019). The analysis was based on Bray-Curtis similarities, using a double Wisconsin standardization on square-root transformed data. Individual PERMANOVAs were conducted to determine if there were differences in fish and benthic communities across seasons, latitude and across the continental shelf.

Benthic Communities

Benthic communities in the low latitude site were different from the mid and high latitude sites driven by the presence of macroalgae, crustose coralline algae (CCA) and soft coral (Figure A6a, Table A8). Benthic communities were all distinct across the continental shelf. Differences in outer shelf benthic communities were driven by the presence of hard coral and CCA, differences to mid-shelf benthic communities were driven by the presence of soft coral and sand, and inner-reef benthic communities were driven by the presence of macroalgae and rubble (Figure A6b, Table A8).

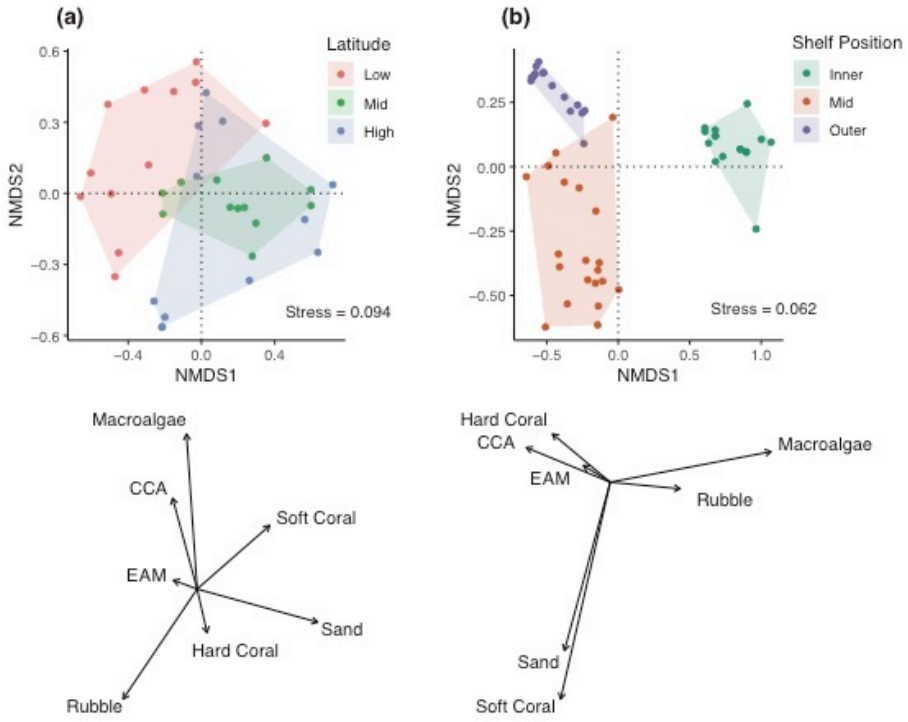

Figure A6: Multidimensional scaling analysis showing the relationship between benthic communities a) across latitude of the GBR and b) across the continental shelf in the northern GBR. Results are based on Bray-Curtis similarities of Wisconsin double standardized and square-root transformed data. Vectors represent partial regression coefficients of the benthic categories within two dimensions.

Table A8: Results of PERMANOVA assessing whether there are differences between benthic communities a) across a latitudinal gradient along the GBR b) across the continental shelf in the northern GBR. Results are significant if $p < 0.05$, and indicated in bold font.

Source	df	MS	F	R^2	p	Bonferroni post-hoc
a) Latitude Comparison						
Latitude	2	0.27	4.65	0.22	**0.001**	**Low ≠ Mid = High**
Residuals	33	0.05		0.78		
Total	35			1.00		
b) Cross-Shelf Comparison						
Shelf position	2	1.95	106.52	0.81	**0.001**	**Inner ≠ Mid ≠ Outer**
Residuals	49	0.01		0.18		
Total	51			1.00		

Herbivore Communities

Herbivorous fish communities were all distinct at each latitude and at each shelf position (Figure A7, Table A9). Across latitude differences at the mid latitude sites were driven by the presence of *Kyphosus* spp. *Naso annulatus* and *Scarus globiceps.* Differences within the low latitude site were driven by the presence of *Ctenochaetus binotatus, Acanthurus nigrofuscus* and *Acanthurus olivaceus.* Across the continental shelf, differences to the inner shelf fish communities were driven by the presence of *Siganus canaliculatus*, *Naso annulatus,* and *Acanthurus grammoptulus.* Differences in mid-shelf reef fish communities were driven by the presence of *Acanthurus olivaceus, Siganus argenteus, Zebrasoma scopas* and *Zebrasoma velliferum*. Differences in outer-shelf fish communities were driven by the presence of *Naso lituratus, Acanthurus lineatus, Acanthurus nigricans* and *Acanthrurus triostegus* (Figure A7, Table A9).

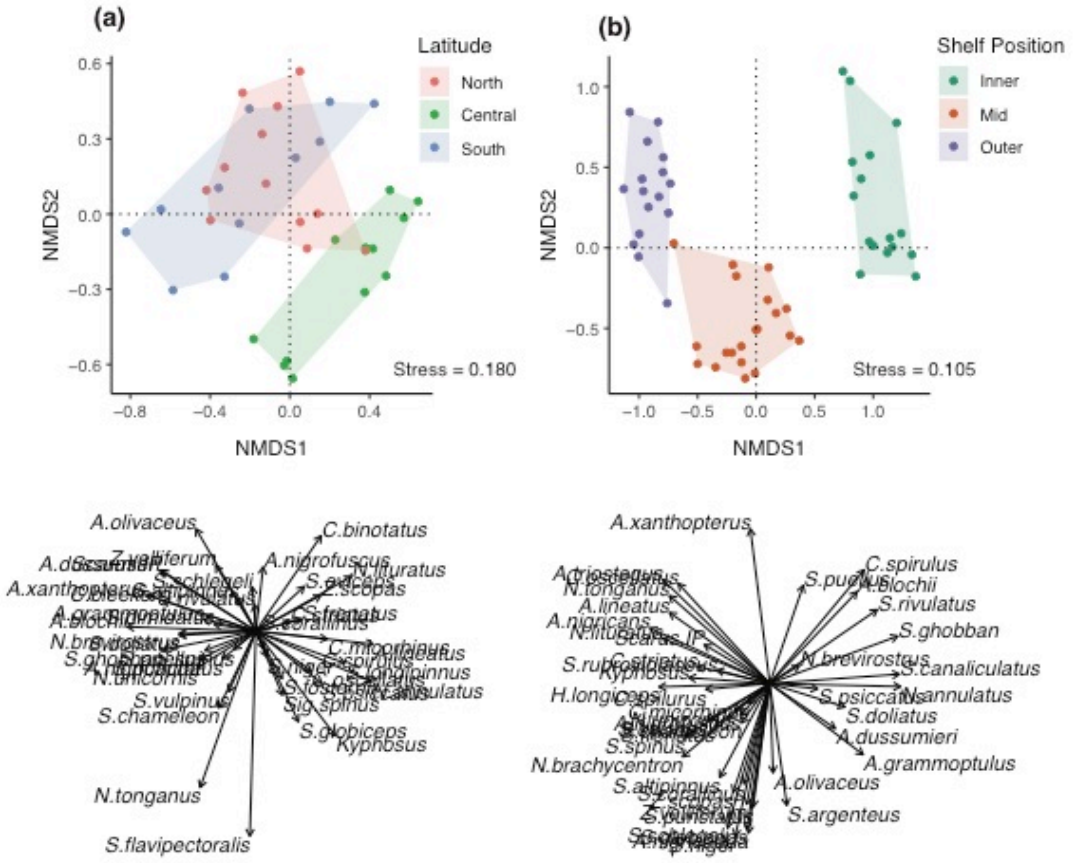

Figure A7: Multidimensional scaling analysis showing the relationship between herbivorous fish communities a) across latitude of the GBR and b) across the continental shelf in the northern GBR. Results are based on Bray-Curtis similarities of Wisconsin double standardized and square-root transformed data. Vectors represent partial regression coefficients of the benthic categories within two dimensions.

Table A9: Results of PERMANOVA assessing whether there are differences between herbivorous fish communities a) across a latitudinal gradient along the GBR b) across the continental shelf in the northern GBR. Results are significant if $p < 0.05$, and indicated in bold font.

Source	df	MS	F	R^2	p	Bonferroni post-hoc
a) Latitude Comparison						
Latitude	2	0.59	3.40	0.17	**0.001**	**Low ≠ Mid ≠ High**
Residuals	32	0.17		0.82		
Total	34			1.00		
b) Cross-Shelf Comparison						
Shelf position	2	3.76	24.61	0.50	**0.001**	**Inner ≠ Mid ≠ Outer**
Residuals	49	0.15		0.50		
Total	51			1.00		

Appendix B: Supporting information for Chapter 3

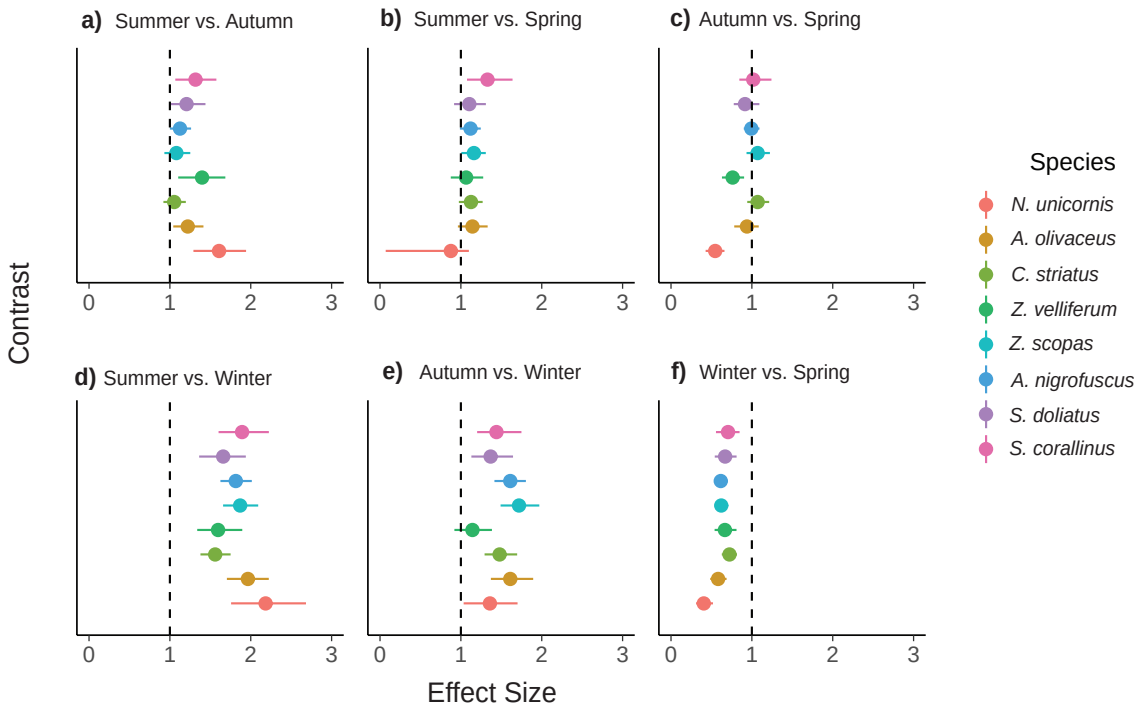

Figure B1: The effect sizes for pairwise comparisons of feeding rates of the local herbivore assemblage for each season. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that feeding rate is greater in the season that is first listed (to the right of the line) or second listed (to the left of the line).

Turf Algae Cover

Site and not season was included as the best fit model for turf algal cover. The cover of turf algae on the reef crest differed among the three sites, but did not differ among seasons. Turf algae cover (mean% [95% credible intervals]) was highest at Palfrey (71.5%[65.70, 78.60]), lowest at North Point (57.4% [50.2, 64.1]) and intermediate at Bird Islet (65.70% [58.60, 71.60]; Fig B2a,b, Table B11).

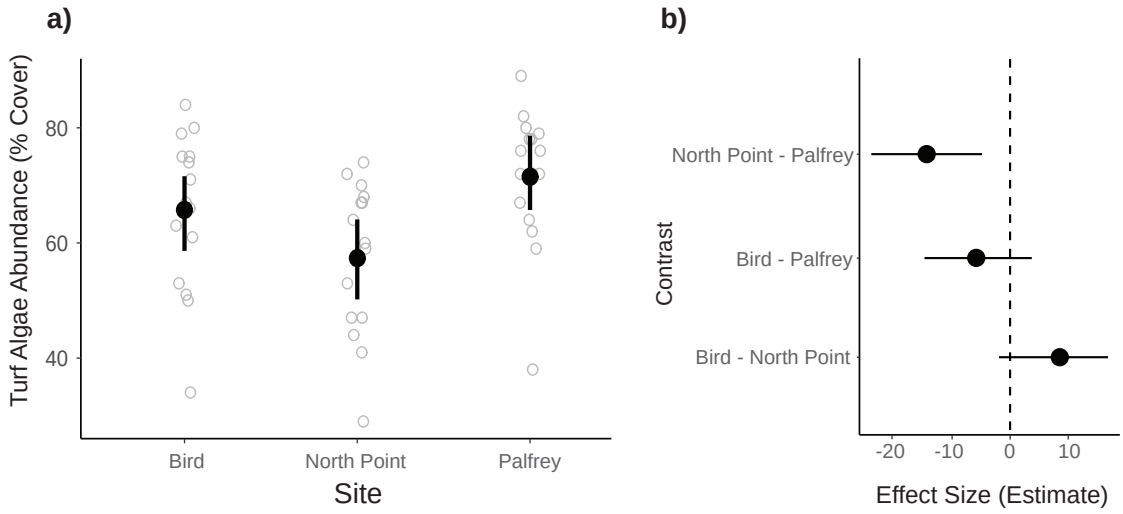

Figure B2: a) EAM abundance (% Cover) from replicate transect surveys across four seasons at three different sites around Lizard Island. Filled circles and lines are mean model estimates ± 95% credible intervals and grey open circles are model residuals. b) The effect sizes for pairwise comparisons of EAM abundance for each season. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that feeding rate is greater in the season that is first listed (to the right of the line) or second listed (to the left of the line).

Turf Algae Cover and Feeding Rates

There was evidence for a positive relationship between turf algae cover and the feeding rates of *Z. velliferum* and *Z. scopas*. Specifically an increase in turf algae cover from 45% to 80% resulted in a 53% increase in the feeding rate of *Z. velliferum* (Figure B3a, Table B6) and a 16% increase in feeding rate of *Z. scopas* (Figure B3b, Table B7).

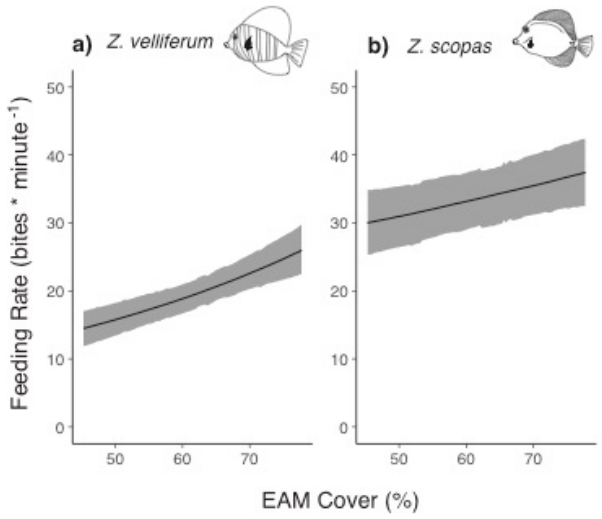

Figure B3: The effect of EAM availability to the feeding rates of a) *Z. velliferum* and b) *Z. scopas*. Lines and ribbons are estimates of Bayesian hierarchical model with gamma distributed errors ± 95% credible intervals.

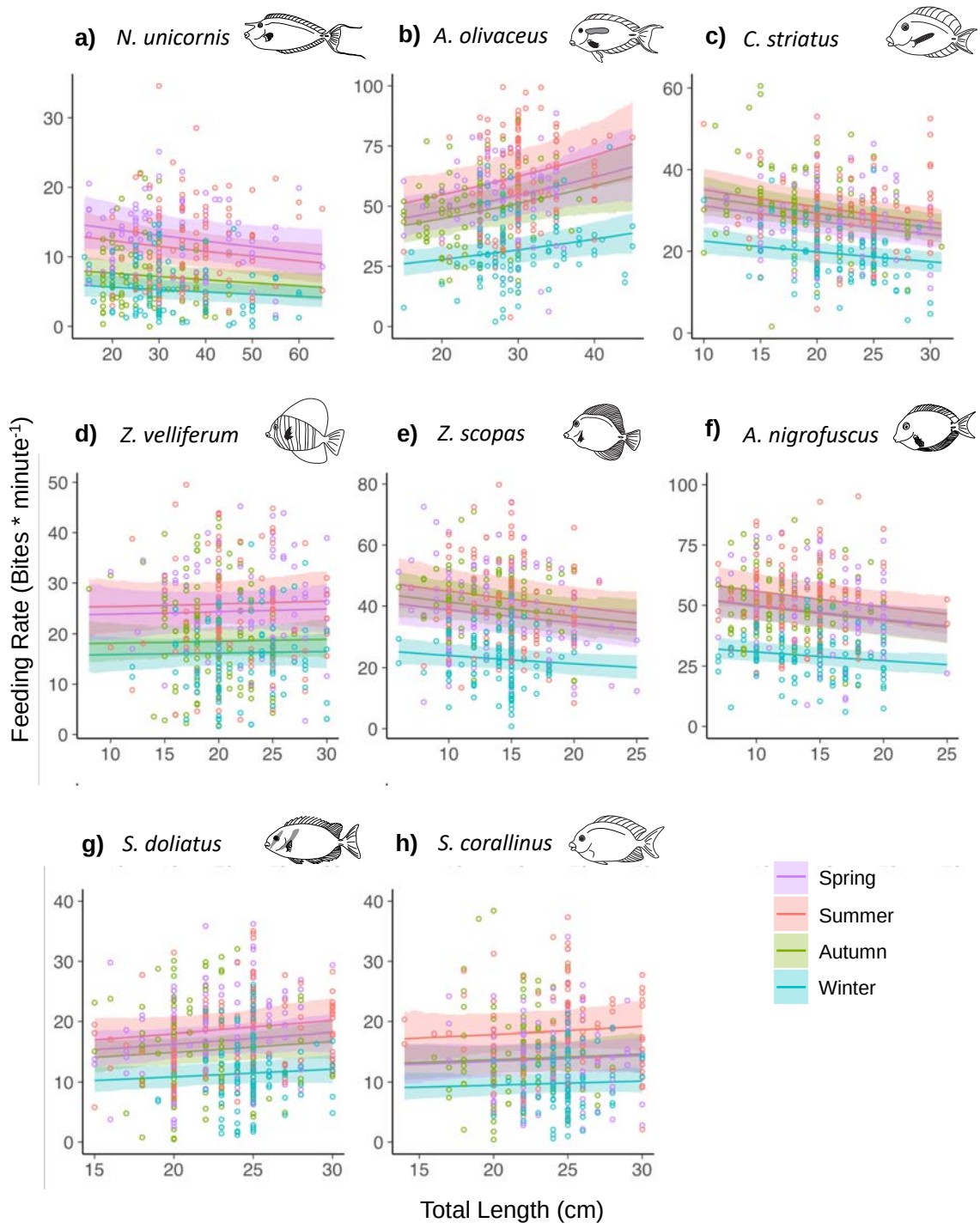

Figure B4: Feeding rates (Bites minute^{-1}) versus body size (Total Length (cm)) of eight herbivorous fishes across four seasons at Lizard Island. Lines and ribbons are estimates of Bayesian hierarchical models ± 95% credible intervals. Open circles are partial residuals of the models.

Table B1: Diet and functional role of eight nominally herbivorous fish species.

Species	Functional group	Diet	Reference(s)
Naso unicornis	Browser	Brown macroalgae (foliose and leathery)	Choat et al., 2002
Acanthurus olivaceous	Detritivore	Detritus, diatoms calcareous sediments	Choat et al., 2002
Ctenochaetus striatus	Detritivore	Detritus, diatoms, calcareous sediments	Choat et al., 2002
Zebrasoma velliferum	Cropper	Green (thallate and filamentous) and red algae (thallate and filamentous)	Guiasu & Winterbottom 1998
Zebrasoma scopas	Cropper	Green (thallate and filamentous) and red algae (thallate and filamentous)	Choat et al., 2002
Acanthurus nigrofuscus	Cropper	Red (filamentous) and green (filamentous) algae, diatoms.	Montgomery et al., 1989
Siganus doliatus	Cropper	Red algae (cortigated, filamentous and foliose), green algae (filamentous), brown algae (foliose)	Hoey et al., 2013
Siganus corallinus	Cropper	Red algae (cortigated, filamentous and foliose), green algae (filamentous), brown algae (foliose and leathery)	Hoey et al., 2013

Table B2: Results of Bayesian generalized linear mixed models with gamma distributed errors for turf algae growth on settlement tiles at three sites around Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	-1.93	0.06	-2.04	-1.81	1.00	3944.00
Season: Spring	-0.09	0.08	-0.24	0.08	1.00	4039.00
Season: Summer	-0.47	0.08	-0.64	-0.32	1.00	4147.00
Season: Winter	-0.20	0.08	-0.36	-0.04	1.00	3847.00
shape	10.69	1.53	7.87	13.67	1.00	3859.00
Sigma	0.01	0.01	0.00	0.02	1.00	3232.00
mean PPD	0.12	0.01	0.11	0.13	1.00	3686.00
log-posterior	164.74	5.62	154.07	175.77	1.00	2816.00

Table B3: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Naso unicornis* over four seasons at Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	2.43	0.12	2.19	2.64	1.00	2296.00
Season: Autumn	-0.48	0.10	-0.67	-0.27	1.00	2387.00
Season: Winter	-0.78	0.11	-0.99	-0.56	1.00	2293.00
Season: Spring	0.13	0.11	-0.09	0.35	1.00	2320.00
Total Length (centred and scaled)	-0.07	0.04	-0.14	0.00	1.00	2327.00
EAM (centred and scaled)	-0.08	0.04	-0.15	0.00	1.00	2293.00
shape	2.77	0.19	2.40	3.14	1.00	2185.00
Sigma	0.10	0.07	0.00	0.25	1.00	2071.00
Mean PPD	9.52	0.42	8.61	10.30	1.00	2386.00
log posterior	-1270.67	5.15	-1280.78	-1261.19	1.00	1722.00

Table B4: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Acanthurus olivaceus* over four seasons at Lizard Island. Results are on the log link scale.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
(Intercept)	4.11	0.08	3.96	4.28	1.00	2170.00
Season: Autumn	-0.20	0.08	-0.36	-0.05	1.00	2320.00
Season: Winter	-0.68	0.07	-0.81	-0.54	1.00	2295.00
Season: Spring	-0.13	0.08	-0.30	0.02	1.00	2354.00
Total Length (centred and scaled)	0.07	0.02	0.02	0.11	1.00	2519.00
% EAM (centred and scaled)	0.03	0.02	-0.02	0.07	1.00	2183.00
shape	6.76	0.45	5.87	7.62	1.00	2489.00
Sigma	0.05	0.03	0.01	0.10	1.00	2047.00
Mean PPD	51.99	1.38	49.17	54.56	1.00	2376.00
log posterior	-1916.05	4.28	-1924.51	-1907.87	1.00	2126.00

Table B5: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Ctenochaetus striatus* over four seasons at Lizard Island. Results are on the log link scale.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
(Intercept)	3.41	0.06	3.30	3.54	1.00	2158.00
Season: Autumn	-0.05	0.07	-0.18	0.08	1.00	2306.00
Season: Winter	-0.44	0.06	-0.57	-0.33	1.00	2261.00
Season: Spring	-0.12	0.07	-0.25	0.02	1.00	2327.00
Total Length (centred and scaled)	-0.06	0.02	-0.09	-0.02	1.00	2340.00
% EAM (centred and scaled)	0.02	0.02	-0.02	0.06	1.00	2537.00
shape	9.23	0.63	8.03	10.46	1.00	2301.00
Sigma	0.02	0.02	0.00	0.05	1.00	2052.00
Mean PPD	27.12	0.61	25.89	28.25	1.00	2287.00
log posterior	-1621.74	4.49	-1630.72	-1613.25	1.00	1929.00

Table B6: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Zebrasoma velliferum* over four seasons at Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	3.25	0.08	3.09	3.41	1.00	2346.00
Season: Autumn	-0.34	0.10	-0.55	-0.13	1.00	2328.00
Season: Winter	-0.47	0.09	-0.64	-0.29	1.00	2296.00
Season: Spring	-0.06	0.10	-0.24	0.13	1.00	2382.00
Total Length (centred and scaled)	0.01	0.03	-0.05	0.07	1.00	2344.00
% EAM (centred and scaled)	0.17	0.03	0.09	0.23	1.00	2300.00
shape	3.60	0.24	3.10	4.05	1.00	2375.00
Sigma	0.02	0.02	0.00	0.06	1.00	1726.00
Mean PPD	21.19	0.78	19.70	22.78	1.00	1933.00
log posterior	-1575.51	4.28	-1583.98	-1567.53	1.00	1705.00

Table B7: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Zebrasoma scopas* over four seasons at Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	3.75	0.08	3.61	3.91	1.00	1986.00
Season: Autumn	-0.08	0.07	-0.23	0.06	1.00	2449.00
Season: Winter	-0.63	0.06	-0.74	-0.51	1.00	2439.00
Season: Spring	-0.15	0.07	-0.27	-0.01	1.00	2482.00
Total Length (centred and scaled)	-0.04	0.02	-0.08	0.00	1.00	2520.00
% EAM (centred and scaled)	0.06	0.02	0.02	0.10	1.00	2406.00
shape	7.92	0.55	6.84	8.95	1.00	2306.00
Sigma	0.04	0.03	0.00	0.09	1.00	2268.00
Mean PPD	37.48	0.93	35.63	39.23	1.00	2342.00
log posterior	-1744.93	4.18	-1753.33	-1737.40	1.00	2034.00

Table B8: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Acanthurus nigrofuscus* over four seasons at Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	3.98	0.06	3.85	4.10	1.00	2219.00
Season: Autumn	-0.12	0.06	-0.23	0.00	1.00	2395.00
Season: Winter	-0.59	0.06	-0.70	-0.49	1.00	2395.00
Season: Spring	-0.11	0.06	-0.22	0.01	1.00	2471.00
Total Length (centred and scaled)	-0.04	0.02	-0.08	-0.01	1.00	2418.00
% EAM (centred and scaled)	0.04	0.02	0.00	0.07	1.00	2274.00
shape	9.59	0.63	8.38	10.89	1.00	2455.00
Sigma	0.02	0.02	0.00	0.06	1.00	2049.00
Mean PPD	46.95	1.04	45.03	49.06	1.00	2443.00
log posterior	-1872.04	4.17	-1880.62	-1864.88	1.00	1995.00

Table B9: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Siganus doliatus* over four seasons at Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	2.93	0.08	2.78	3.08	1.00	2277.00
Season: Autumn	-0.19	0.09	-0.37	-0.01	1.00	2259.00
Season: Winter	-0.50	0.09	-0.67	-0.32	1.00	2351.00
Season: Spring	-0.10	0.09	-0.28	0.08	1.00	2179.00
Total Length (centred and scaled)	0.04	0.03	-0.01	0.09	1.00	2341.00
EAM (centred and scaled)	0.03	0.03	-0.03	0.09	1.00	2549.00
shape	4.08	0.25	3.58	4.57	1.00	2210.00
Sigma	0.02	0.02	0.00	0.05	1.00	2174.00
Mean PPD	16.02	0.52	15.02	17.11	1.00	2465.00
log posterior	-1649.03	4.38	-1657.52	-1640.66	1.00	1736.00

Table B10: Results of Bayesian hierarchical models with gamma distributed errors for the feeding rate of *Siganus corallinus* over four seasons at Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	2.91	0.09	2.75	3.08	1.00	2233.00
Season: Autumn	-0.27	0.10	-0.45	-0.06	1.00	2264.00
Season: Winter	-0.64	0.09	-0.80	-0.47	1.00	2350.00
Season: Spring	-0.29	0.11	-0.50	-0.08	1.00	2156.00
Total Length (centred and scaled)	0.02	0.03	-0.03	0.08	1.00	2323.00
% EAM (centred and scaled)	0.04	0.03	-0.03	0.10	1.00	2415.00
shape	4.13	0.29	3.61	4.72	1.00	2152.00
Sigma	0.04	0.03	0.00	0.09	1.00	2223.00
Mean PPD	14.45	0.52	13.45	15.45	1.00	2246.00
log posterior	-1353.97	4.30	-1362.91	-1346.05	1.00	2042.00

Table B11: Results of Bayesian generalized linear mixed models with gamma distributed errors for total bites per hour taken by the local herbivore assemblage on 1 m^2 benthic substrata with <10% coral cover at three sites around Lizard Island. Results are on the log link scale.

Term	Estimate	SE	Lower CI	Upper CI	rhat	ess
(Intercept)	5.20	0.26	4.65	5.68	1.00	2286.00
Season: Spring	0.87	0.33	0.23	1.53	1.00	2180.00
Season: Summer	1.08	0.32	0.49	1.73	1.00	2248.00
Season: Winter	0.34	0.34	-0.32	1.01	1.00	2081.00
shape	1.03	0.14	0.77	1.31	1.00	2454.00
Mean PPD	389.20	62.92	265.83	508.34	1.00	2202.00
log-posterior	-618.86	1.62	-622.05	-616.50	1.00	2379.00

Table B12: Results of Bayesian hierarchical models with gaussian distributed errors for Percent Cover of EAM at three sites over four seasons at Lizard Island. Results are on the natural scale.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
(Intercept)	65.67	3.35	58.62	71.59	1.00	904.00
Site: North Point	-8.29	4.86	-16.85	2.01	1.00	898.00
Site: Palfrey	5.94	4.68	-3.72	14.88	1.00	977.00
Sigma	13.05	1.43	10.55	16.09	1.00	942.00
Mean PPD	64.89	2.76	59.32	69.97	1.00	1169.00
log posterior	-196.02	1.61	-199.18	-193.99	1.00	844.00

Table B13: Results of PERMANOVA assessing whether there are differences between a) fish communities and b) benthic communities of the three study sites at Lizard Island. Results are significant if $p < 0.05$, and indicated in bold font.

Source	df	SS	MS	F	R^2	p
a) Fish communities						
Site	2	1.7993	0.8996	7.7107	0.2303	**0.001**
Season	3	0.6830	0.2277	1.9513	0.0874	**0.003**
Site*Season	6	1.2641	0.2077	1.7801	0.1595	**0.001**
Residuals	35	6.0126	0.1367		0.5227	
Total	46	7.8119			1.00	
b) Benthic communities						
Site	2	1.3770	0.6885	5.7230	0.1763	**0.001**
Season	3	0.6720	0.2240	1.8620	0.0860	**0.006**
Site*Season	6	1.5521	0.2587	2.1502	0.1987	**0.001**
Residuals	35	4.2107	0.1203		0.5390	
Total	46	7.8119			1.00	

Appendix C: Supporting information for Chapter 4

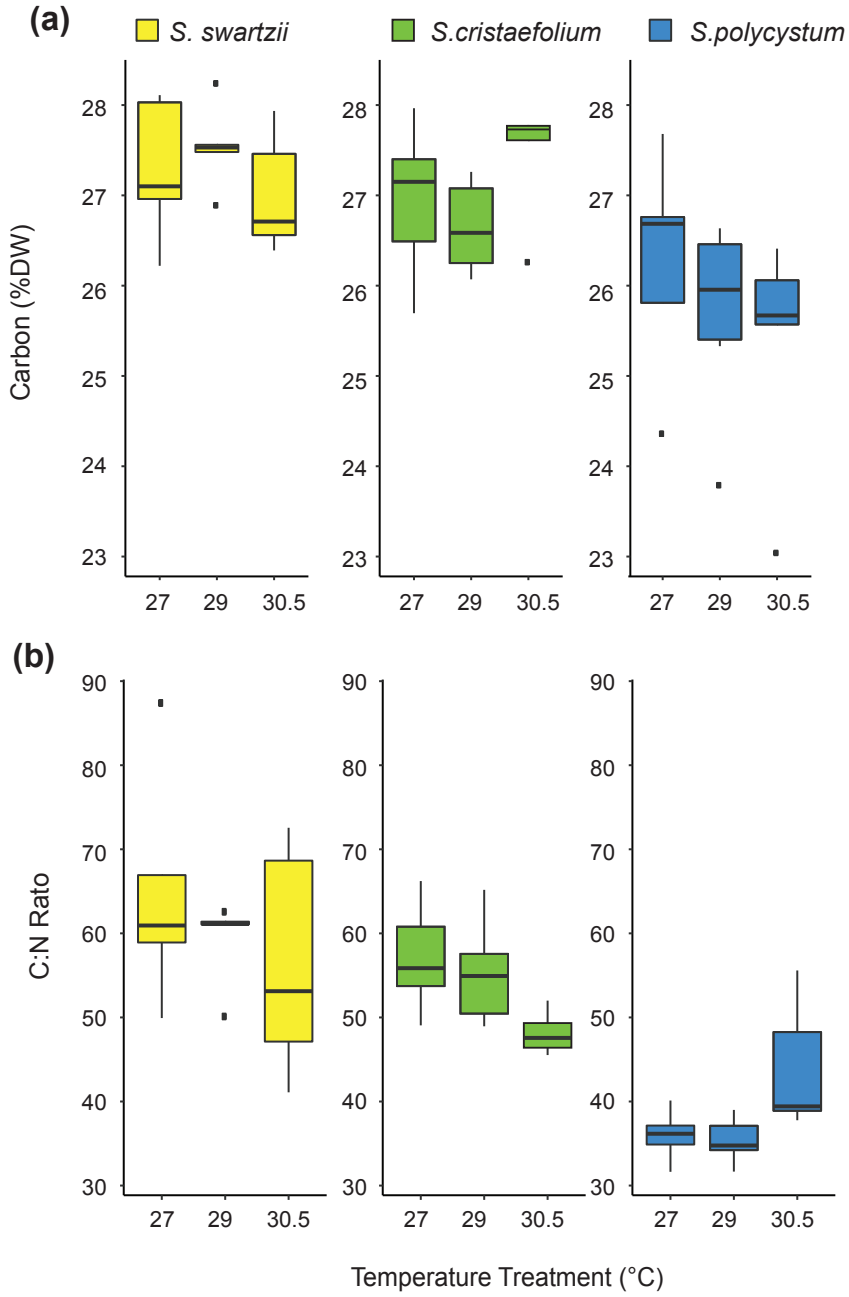

Figure C1: Comparison of the a) carbon content and b) the C:N ratio of three species of tropical *Sargassum* (*S. swartzii*, *S. cristaefolium*, and *S. polycystum*) cultured at different water temperatures for two weeks.

Table C1: Akaike Information Criteria (AICc) comparing generalized linear mixed effects models and linear mixed effects models for the response of different parameters of juvenile *Sargassum* to different temperature treatments. An asterisk indicated the smaller AICc value and the model that best predicts the data. Bold values indicate where the best fitted model includes temperature as a fixed factor.

Parameter	Model		df	AICc
	Fixed Factor	Random Factor		
Survival	-	-	1	2748.836
	Time	Tank	3	1240.809
	Temperature	Tank	4	2343.300
	Temperature + Time	Tank	5	1230.780
	Temperature * Time	Tank	7	**1201.391***
Relative Growth Rate†	-	-	1	454.5247
	Time	Tank	4	188.8774
	Temperature	Tank	5	449.4213
	Temperature + Time	Tank	6	**167.3286***
	Temperature * Time	Tank	8	168.1988

† Data was log(100 + x) transformed

Table C2: Summary for all Tukey's *post-hoc* Pairwise tests for multiple comparisons of different parameters of *Sargassum* propagules to different temperature treatments. Significant results indicated by a *. Survival data is back-transformed to the natural scale using a logit link function.

Parameter	Factor	Contrast	Odds ratio	SE	df	z-ratio	p
Survival	Temperature at 5 days	Amb vs +2ºC	0.79	0.156	Inf	-1.19	0.46
		Amb vs +3.5ºC	1.33	0.262	Inf	1.421	0.33
		+3.5ºC vs + 2ºC	0.596	0.10	Inf	-2.96	0.009*
	Temperature at 48 days	Amb vs +2ºC	0.76	0.18	Inf	-1.16	0.47
		Amb vs +3.5ºC	5.09	1.643	Inf	5.05	0.001*
		+3.5ºC vs + 2ºC	0.15	0.05	Inf	-6.17	0.001*
Parameter	Factor	Contrast	Estimate	SE	df	t-ratio	p
Relative Growth Rate (%)	Temperature at 5 and 48 days (no interaction)	Amb vs +2ºC	0.08	0.04	266	1.803	0.17
		Amb vs +3.5ºC	0.24	0.05	266	5.1	0.001*
		+3.5ºC vs + 2ºC	-0.16	0.05	266	-3.40	0.002*
	Time	5 days vs 48 days	0.84	0.04	266	22.35	0.001*

Table C3: Akaike Information Criteria (AICc) comparing linear and linear mixed effects models for the response of different parameters of adult *Sargassum* to different temperature treatments. An asterisk indicated the smallest AICc value and the model that best predicts the data. Bold values indicate where the best fitted model includes temperature as a fixed factor. DNC: Did not converge

Parameter	Model		df	*S. swartzii*	*S. cristaefolium*	*S. polycystum*
	Fixed	Random				
Relative Growth Rate	-	Tank	4	380.3789	388.9041	406.630
	Temp	Tank	5	**366.6773***	**375.3759***	**388.944***
	Temp	Temp | Tank	10	381.1136	DNC	DNC
Physical Toughness	-	Tank/Ind	4	1890.670	2051.129	1838.781
	Temp	Tank /Ind	6	**1871.796***	**2023.379***	**1821.115***
	Temp	Temp | (Tank /Ind)	16	DNC	DNC	1840.959
Nitrogen	-	-	2	-27.7962*	-36.7677	-26.6039
	Temp	-	4	-22.3867	**-38.3736***	**-32.3521***
Carbon	-	-	2	33.4767*	38.7171*	54.8025*
	Temp	-	4	38.5653	41.4988	59.8357
C:N Ratio	-	-	2	119.95*	96.47026*	104.5693*
	Temp	-	4	124.93	97.8251	106.992
Mass removed by herbivores (g)	-	Rope	3	193.3434	193.7056	139.8248*
	Temp	Rope	5	**184.4700***	**185.7776***	138.0134

Table C4: Summary for all Tukey's *post-hoc* Pairwise tests for all multiple comparisons of different parameters of adult and juvenile *Sargassum* to different temperature treatments, where temperature was included in the best fit model (See Table S3). Significant results indicated by a *.

Parameter	Species	n	Comparison	Test statistic	Tukey's p
Relative Growth Rate (%)	*S. swartzii*	14-15	+3.5ºC vs Ambient	-2.343	0.05*
			+2ºC vs Ambient	0.312	0.95
			+2ºC vs +3.5ºC	2.655	0.02*
	S. cristaefolium	15	+3.5ºC vs Ambient	-2.42	0.04*
			+2ºC vs Ambient	0.18	0.98
			+2ºC vs +3.5ºC	2.60	0.03*
	S. polycystum	13-15	+3.5ºC vs Ambient	-3.171	0.005*
			+2ºC vs Ambient	-2.963	0.009*
			+2ºC vs +3.5ºC	0.249	0.967
Physical Toughness (g)	*S. swartzii*	43-45	+3.5ºC vs Ambient	0.719	0.859
			+2ºC vs Ambient	1.564	0.461
			+2ºC vs +3.5ºC	0.853	0.783
	S. cristaefolium	45	+3.5ºC vs Ambient	-2.497	0.009*
			+2ºC vs Ambient	-0.017	0.998
			+2ºC vs +3.5ºC	2.930	0.010*
	S. polycystum	39-45	+3.5ºC vs Ambient	-0.125	0.991
			+2ºC vs Ambient	0.068	0.994
			+2ºC vs +3.5ºC	0.191	0.972
Nitrogen (%)	*S. cristaefolium*	5	+3.5ºC vs Ambient	2.757	0.043*
			+2ºC vs Ambient	0.251	0.966
			+2ºC vs +3.5ºC	-2.507	0.066
	S. polycystum	5	+3.5ºC vs Ambient	-3.353	0.013*
			+2ºC vs Ambient	-0.028	0.996
			+2ºC vs +3.5ºC	3.474	0.011*
Mass Removed by Herbivores (g)	*S. swartzii*	8	+3.5ºC vs Ambient	-3.091	0.006*
			+2ºC vs Ambient	-1.587	0.251
			+2ºC vs +3.5ºC	1.504	0.289
	S. cristaefolium	10	+3.5ºC vs Ambient	-2.520	0.032*
			+2ºC vs Ambient	-2.407	0.043*
			+2ºC vs +3.5ºC	0.113	0.993

Table C5: Akaike Information Criteria (AICc) comparing linear mixed effects models for the mass standardized bites from fish from the local herbivore assemblage exposed to thalli grown in different temperature treatments. An asterisk indicated the smallest AICc value and the model that best predicts the data. Bold values indicate where the best fitted model includes temperature as a fixed factor.

		Model			
Seaweed	Fish	Fixed	Random	df	AICc
S. swartzii†	*S. doliatus*	-	Rope	3	-67.6904*
		Temperature	Rope	5	48.5054
	N. unicornis	-	Rope	3	-30.5430*
		Temperature	Rope	5	-14.9600
	other	-	Rope	3	-18.5370*
		Temperature	Rope	5	10.70815
S. cristaefolium¥	*S. doliatus*	-	Rope	3	-38.1715*
		Temperature	Rope	5	-25.3218
	N. unicornis	-	Rope	3	-17.9217*
		Temperature	Rope	5	-3.4627
	other	-	Rope	3	-14.9939*
		Temperature	Rope	5	-0.641982
S. polycystum¥	*S. doliatus*	-	Rope	3	-12.4687*
		Temperature	Rope	5	-0.2605
	N. unicornis	-	Rope	3	6.2426*
		Temperature	Rope	5	29.4663
	other	-	Rope	3	7.0196*
		Temperature	Rope	5	19.1323

† data are log (1+x) transformed

¥ data are sqrt(x) transformed

Table C6: Mean mass standardized bites (bites g fish^{-1}) and standard errors from the local herbivore assemblage on three different species of *Sargassum* grown in different temperature treatments. n is the number of trials (ropes) each fish species was present and took bites from any experimental thalli.

Species	**Temperature Treatment**	**fish**	**n**	**mean bites**	**SE**
S. swartzii	Ambient (27°C)	all	8	0.19	0.11
		S. doliatus	7	0.05	0.03
		N. unicornis	8	0.13	0.10
		other	3	0.03	0.03
	+2°C	all	8	0.13	0.05
		S. doliatus	7	0.04	0.02
		N. unicornis	8	0.08	0.05
		other	3	0.04	0.04
	+3.5°C	all	8	0.15	0.07
		S. doliatus	7	0.03	0.01
		N. unicornis	8	0.12	0.07
		other	3	0.01	0.01
S. cristaefolium	Ambient (27°C)	all	10	0.09	0.02
		S. doliatus	7	0.05	0.01
		N. unicornis	5	0.02	0.01
		other	6	0.07	0.03
	+2°C	all	10	0.10	0.03
		S. doliatus	7	0.03	0.01
		N. unicornis	5	0.04	0.03
		other	6	0.09	0.06
	+3.5°C	all	10	0.07	0.03
		S. doliatus	7	0.03	0.01
		N. unicornis	5	0.01	0.00
		other	6	0.07	0.05
S. polycystum	Ambient (27°C)	all	9	0.19	0.08
		S. doliatus	8	0.10	0.03
		N. unicornis	3	0.03	0.02
		other	5	0.16	0.15
	+2°C	all	9	0.13	0.06
		S. doliatus	8	0.10	0.05
		N. unicornis	3	0.07	0.07
		other	5	0.02	0.02
	+3.5°C	all	9	0.09	0.02

		S. doliatus	8	0.06	0.02
		N. unicornis	3	0.01	0.00
		other	5	0.06	0.03

Appendix D: Supporting information for Chapter 5

Experimental Recirculating Seawater System and Temperature Manipulation

Experimental water for the 26°C treatment was manipulated using a Toyesi heat pump (± 0.5°C) in a 2,800L sump, which then fed into three 380 L sumps and using 3KW steel bar heaters, with one sump per temperature treatment. Each sump was supplied with recirculating filtered seawater at a rate of 270 L hr^{-1} and supplied 7 (for the 28°C and 32°C temperature treatments) and 8 (for the 26°C and 30°C treatments) replicate 72 L aquaria with the appropriate experimental seawater using 1000L hr^{-1} pumps (Eheim) at an average rate across tanks of 103.36 ± 1.6 SE L hr^{-1}. Recirculating seawater was filtered using an oversized (300mm x 1600mm) foam fractionator supplied with air from a 20 mm Mazzi venturi to remove organic compounds. An upwelling tower (300mm diameter x 1500 mm high) filled with 110 L of K2 Media was used for biological filtration. Lastly, recirculating seawater was filtered through two 50 micron filter bags (C50 Waterco filter housings) to remove particulate matter prior to being supplied to the experimental system. Temperature was controlled using digital thermostats (TIC-17RGT, Full Gauge), which recorded temperature every hour to an internal log, and was calibrated weekly.

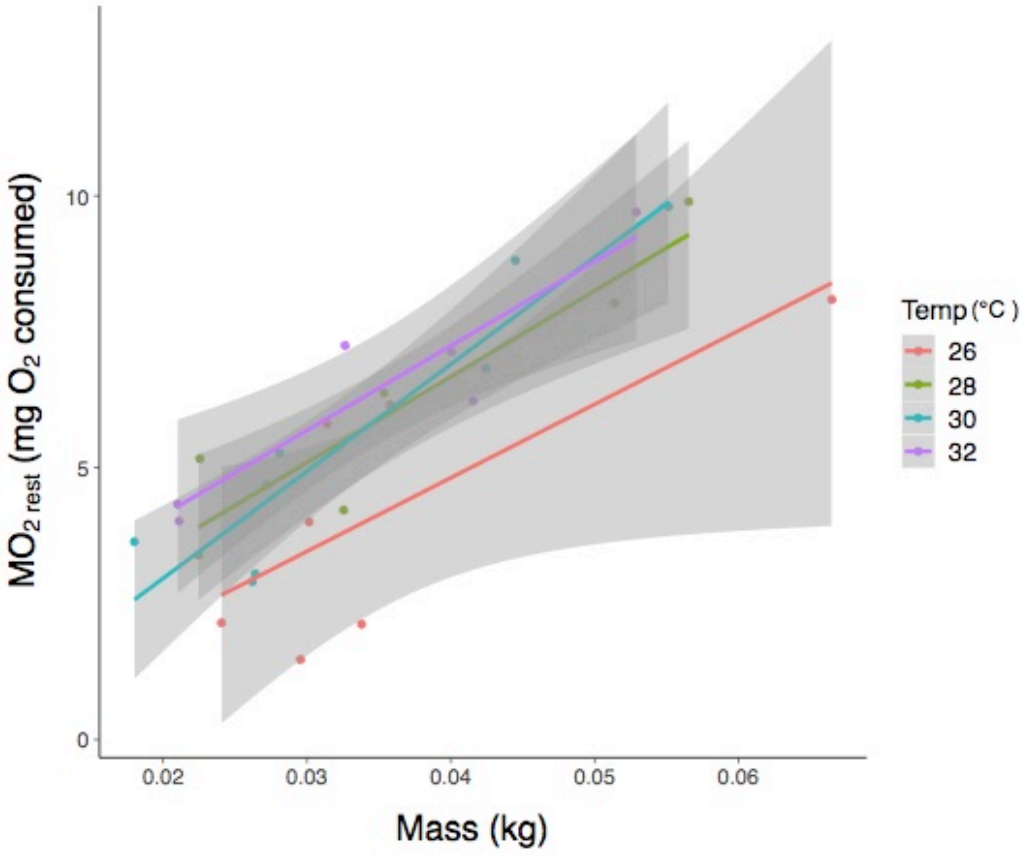

Figure D1: Linear relationship between individual mass (kg) and $MO_{2\ rest}$ (mg O_2 consumed per fish). Lines and ribbons were fit with a linear smoother.

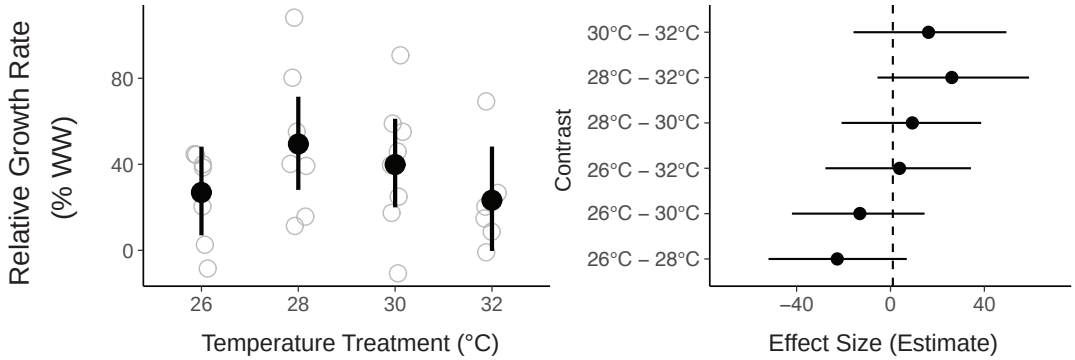

Figure D2: Relative Growth rate as % Wet Weight (WW: g) of individual juvenile *Siganus doliatus* reared in four different temperature treatments. Solid circles and lines are mean model estimates ± 95% credible intervals, and open grey circles are partial residuals of the models. Associated effect sizes for pairwise contrasts for RGR. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that there is an effect for RGR in the temperature that is first listed (to the right of the line) or second listed (to the left of the line).

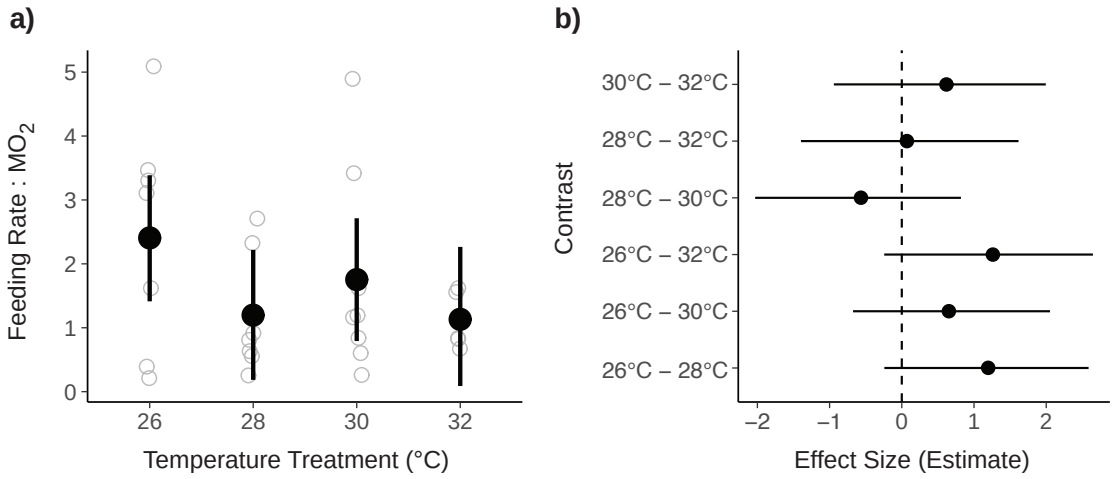

Figure D3: a) Feeding Rate vs $MO_{2\ rest}$ ratio for juvenile *S. doliatus* reared in four different temperature treatments. Filled circles and lines are mean model estimates ± 95% credible intervals, open grey circles are partial residuals of the model. b) Effect sizes for pairwise contrasts for Feeding Rate: MO_2 ratio. When 95% Bayesian credible intervals (CI) do not overlap the vertical dotted line, there is strong evidence that there is an effect for the ratio in the temperature that is first listed (to the right of the line) or second listed (to the left of the line).

Table D1: Leave One Out Information Criteria (LOOIC) comparing linear models for the initial size (Wet Weight (g), Total Length (cm) of juvenile *Siganus doliatus* prior to being exposed to one of four temperature treatments. An asterisk indicated the smallest LOOIC value and the model that best predicts the data.

Parameter	Model		LOOIC	
	Fixed	Random	Estimate	SE
Initial Wet Weight	-	-	246.7*	9.6
	Temperature	-	253.1	1.4
Initial Total Length	-	-	116.2*	6.5
	Temperature	-	122.7	7.4

Table D2: Results of Bayesian generalized linear models with gaussian (RMR and RGR) and gamma (Feeding rate and HI) distributed errors for a) feeding rate, b) RMR, c) RGR (%WW), d) RGR (%TL) and e) HI of juvenile *S. doliatus* reared in four different temperature treatments. Gamma models are on the link (log) scale. Gaussian models are on the natural scale

Parameter	**Term**	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
a) Resting Metabolic Rate	(Intercept)	118.90	14.57	91.85	148.66	1.00	3947.00
	Temp: 28°C	50.26	21.04	8.40	92.18	1.00	4059.00
	Temp: 30°C	45.84	19.76	5.03	82.67	1.00	4216.00
	Temp: 32°C	68.01	21.25	24.98	108.40	1.00	4193.00
	shape	38.63	5.72	28.29	50.20	1.00	4414.00
	mean PPD	158.91	10.52	138.45	179.15	1.00	4371.00
	log posterior	-152.98	1.73	-156.30	-150.32	1.00	3682.00
b) Feeding Rate	(Intercept)	5.45	0.30	4.88	6.06	1.00	3518.00
	Temp: 28°C	-0.09	0.44	-0.95	0.75	1.00	3456.00
	Temp: 30°C	0.31	0.41	-0.55	1.11	1.00	3569.00
	Temp: 32°C	-0.18	0.41	-1.05	0.55	1.00	3621.00
	shape	1.72	0.44	0.91	2.59	1.00	3990.00
	mean PPD	252.25	57.43	148.27	362.18	1.00	3941.00
	log posterior	-193.10	1.74	-196.45	-190.51	1.00	3279.00
c) Relative Growth Rate (% WW)	(Intercept)	26.89	10.92	5.41	48.68	1.00	3633.00
	Temp: 28°C	22.66	15.46	-7.06	54.27	1.00	3991.00
	Temp: 30°C	13.13	14.79	-16.42	41.60	1.00	3827.00
	Temp: 32°C	-3.53	15.62	-33.42	28.36	1.00	4035.00
	shape	29.25	4.33	21.61	37.99	1.00	3774.00
	mean PPD	35.28	7.94	20.16	51.82	1.00	4607.00
	log posterior	-144.51	1.69	-147.89	-142.05	1.00	3484.00
d) Relative Growth Rate (%TL)	(Intercept)	4.80	3.15	-1.40	10.96	1.00	3593.00
	Temp: 28°C	11.41	4.39	2.65	19.93	1.00	4179.00
	Temp: 30°C	5.95	4.29	-2.75	14.19	1.00	4062.00
	Temp: 32°C	0.09	4.64	-9.54	8.63	1.00	3999.00
	shape	8.43	1.22	6.25	10.89	1.00	3993.00
	mean PPD	9.36	2.30	4.94	14.08	1.00	4529.00
	log posterior	-108.51	1.72	-111.86	-105.98	1.00	3682.00
e) Hepatosomatic Index (HI)	(Intercept)	-4.08	0.05	-4.19	-3.97	1.00	3545.00
	Temp: 28°C	-0.10	0.08	-0.25	0.05	1.00	3391.00
	Temp: 30°C	-0.28	0.08	-0.42	-0.13	1.00	3638.00
	Temp: 32°C	-0.11	0.08	-0.26	0.04	1.00	3602.00
	shape	50.41	13.81	25.20	78.37	1.00	3954.00
	mean PPD	0.01	0.00	0.01	0.02	1.00	4084.00
	log posterior	129.61	1.75	126.10	132.12	1.00	3045.00

Table D3: Results of Bayesian generalized linear models with gamma distributed errors for a) feeding rate for the feeding selectivity of juvenile *S. doliatus* reared in four different temperature treatments. Results are on the log-link scale.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	**rhat**	**ess**
(Intercept)	3.52	0.34	2.85	4.17	1.00	3180.00
Temp: 28°C	-0.39	0.52	-1.42	0.63	1.00	3624.00
Temp: 30°C	0.19	0.48	-0.74	1.16	1.00	3314.00
Temp: 32°C	-0.11	0.48	-1.05	0.81	1.00	3199.00
Food: *Padina*	0.26	0.49	-0.73	1.18	1.00	3270.00
Food: *Sargassum*	0.19	0.49	-0.76	1.13	1.00	3415.00
Temp 28°C:Food *Padina*	0.64	0.73	-0.83	2.04	1.00	3631.00
Temp 30°C:Food *Padina*	-0.10	0.68	-1.35	1.29	1.00	2877.00
Temp 32°C:Food *Padina*	0.28	0.67	-1.02	1.55	1.00	3364.00
Temp 28°C:Food *Sargassum*	0.35	0.74	-1.02	1.86	1.00	3615.00
Temp 30°C: Food *Sargassum*	-0.38	0.68	-1.70	0.93	1.00	3481.00
Temp 32°C: Food *Sargassum*	-0.10	0.67	-1.48	1.17	1.00	3379.00
shape	1.02	0.14	0.75	1.30	1.00	3879.00
mean_PPD	42.67	7.46	28.59	57.08	1.00	4012.00
log-posterior	-420.06	2.74	-425.03	-415.09	1.00	3394.00